Tool innovation may be a critical limiting step for the establishment of a rich tool-using culture: A perspective from child development

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DOI:
10.1017/S0140525X11001877

BEHAVIORAL AND BRAIN SCIENCES (2012), Page 1 of 60
doi:10.1017/S0140525X11001452

The cognitive bases of human tool use

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Abstract: This article has two goals. The first is to assess, in the face of accruing reports on the ingenuity of great ape tool use, whether and in what sense human tool use still evidences unique, higher cognitive ability. To that effect, I offer a systematic comparison between humans and nonhuman primates with respect to nine cognitive capacities deemed crucial to tool use: enhanced hand-eye coordination, body schema plasticity, causal reasoning, function representation, executive control, social learning, teaching, social intelligence, and language. Since striking differences between humans and great apes stand firm in eight out of nine of these domains, I conclude that human tool use still marks a major cognitive discontinuity between us and our closest relatives. As a second goal of the paper, I address the evolution of human technologies. In particular, I show how the cognitive traits reviewed help to explain why technological accumulation evolved so markedly in humans, and so modestly in apes.

Keywords: cognition; evolution; great apes; technology; tool use; cumulative culture

1. Introduction

Ever since Jane Goodall's observations of ant-dipping chimpanzees some 50 years ago, the idea that human tool use evidences "humanique" cognitive ability has lost popularity. To date, chimpanzees have been demonstrated to use "complex toolkits" (Fowler & Sommer 2007; Sanz & Morgan 2007), "complex toolsets" (Sanz et al. 2009; Boesch et al. 2009), and "composite technologies" (Carvalho et al. 2009) – behaviors that, according to many, indicate that chimpanzees share with humans at least the cognitive machinery for dealing with their physical world (see, e.g., Hrdy 2009; Tomasello & Hermann 2010). To the extent that human tool use still evidences cognitive superiority, that superiority is said to be found in the social domain: The remarkable complexity of human technologies attests to more sophistication in matters of imitation, teaching, and participation in collaborative activities. It is these capacities (rather than individual brainpower) that, through cumulative evolution, gave rise to our astonishing technological achievements (see e.g., Boyd & Richerson 1996; Herrmann et al. 2007; Richerson & Boyd 2005; Tomasello et al. 2005).

In this paper, I show that it is a mistake to discard tool use as a hallmark of human cognition. Human tool use reflects higher social intelligence (indeed), but just as much greater non-social wit. In support of my argument, I offer a systematic comparison between humans and nonhuman primates with respect to nine cognitive capacities (both social and non-social) deemed crucial to tool use: enhanced hand-eye coordination (sect. 2), body schema plasticity (sect. 3), causal reasoning (sect. 4), function representation (sect. 5), executive control (sect. 6), social learning (sect. 7), teaching (sect. 8), social intelligence (sect. 9), and language (sect. 10).[1] Because striking differences between humans and great apes stand firm in eight out of nine of these domains (see Table 2, for a more detailed and balanced overview), I conclude that human tool use still marks a major cognitive discontinuity between us and our closest relatives; and relatedly, that no individual cognitive trait can be singled out as the key trait differentiating humans from other animals.[2]

As a second aim of the paper, I make clear how several of the cognitive traits reviewed help to explain our unique ability for cumulative culture, as well as the astonishing technological complexity this has produced (sect. 12). I show how some traits enable high-fidelity cultural transmission, yielding preservation of traits across successive generations; and how others, by facilitating individual learning, further the introduction of new cultural variants, necessary for incremental change. Given that chimpanzees lack many of these traits, much of the vast discrepancy between human and chimp technologies is thereby explained.

2. Hand-eye coordination

Chimpanzees display quite complex manual skills. Byrne (2004), for example, notes that chimpanzees share with humans the use of precision grips, asymmetrical and bimanual tool use, and even strong individual lateralities (preference for one hand to perform the same task).

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 0140-525X/12 $40.00

Three lines of evidence, however, support the idea of superior hand-eye coordination in humans.[3] First, more neural tissue is devoted to the human hand than to the hand of chimpanzees; chimpanzees have much smaller amounts of gray matter controlling their limb movements (MacLarnon 1996) than humans do. This means they face more difficulties in inhibiting the contraction of muscle fibers. Instead of a successive and orderly recruitment of their motor units, chimpanzees are forced to recruit larger numbers of units at once. As Walker (2009) notes, this lack of cerebral inhibition endows chimpanzees with a remarkable strength, at the expense, however, of fine motor control.

The second line of evidence comes from two strands of brain research. First, Orban and colleagues (2006) identified a set of functional regions in the dorsal intraparietal sulcus (IPS) of the human brain that is involved in representations of the central visual field and in the extraction of three-dimensional form from motion. Crucially, these brain regions were not found in the brains of monkeys. The regions subserve, the authors conjectured, the enhanced visual analysis necessary for the precision with which humans manipulate tools. Second, Stout and Chaminade (2007) found that parts of these regions were indeed recruited when modern human subjects engaged in Oldowan-like tool making. Importantly, no increased activation was observed when the human subjects were asked just to strike cobbles together without intending to produce flakes. Human dorsal IPS, thus, may allow for better identification of suitable targets on the core, and as such, explain in part why humans outperform other primates in matters of tool use.[4]

The third line of evidence relates to handedness – a population-wide preference for one hand, such as the 85–90% right-handedness in the human population (e.g., Raymond & Pontier 2004). Although it is true that chimpanzees exhibit individual and population-level hand biases for some tasks,[5] the fact remains that, in the light of current evidence, the ratio of right- to left-handedness is much lower in great apes compared with humans; and that ambidextrousness is much more common in chimpanzee than human populations.[6]

How do handedness and enhanced hand-eye coordination relate? There are two plausible ways. First, lateralization enhances manual precision. McGrew and Marchant (1999), for example, observe that exclusively lateralized chimpanzees are more able termite fishers than are weakly handed or ambidextrous individuals. Second, handedness probably facilitates motor coordination in social learning tasks. When all individuals in a population are handed alike, a learner can directly copy the model's hand configuration (i.e., without having to project it to the opposing hand) (e.g., Michel & Harkins 1985; Uomini 2009).

Summary: Enhanced hand-eye coordination relates to the fact that (1) in humans, more neural tissue is devoted to the hands; (2) humans possess brain structures for higher-order visual analysis, involved in affordance discovery and exploitation; and (3) our species' handedness makes for higher manual precision and smoother social learning.

3. Body schema plasticity

To guide actions in space, the brain needs to keep track of any changes in body shape and posture, and it does so by updating its representation of the body – aka the body schema. It long has been suggested that the body schema is plastic, in the sense that it can incorporate external objects.[7] A hand-held tool, for example, may become so familiar to the user that it at least feels as if it is a natural extension of the hand. The ramifications for tool use are evident: Better tool assimilations should yield more fluent tool use. Body schema plasticity, then, might be another factor making human tool use unique.

Now there is strong evidence that the human brain indeed can and does represent external aids as belonging to the body. The evidence comes from (1) crossmodal interference tasks in healthy humans and from (2) studies on patients with unilateral spatial neglect or (3) extinction.[8] In all these experiments, subjects were asked to operate simple tools, such as canes, rakes, and golf clubs. Interestingly, it appears that tool assimilation is contingent on the functional properties of the tool. Farnè and colleagues (2005), for example, show that only the effective length of a tool gets incorporated, not its absolute length. So, if a 60-cm-long tool has its functional part (say, a hook for grasping) at 20 cm (making the other 40 cm of the tool functionally redundant), only the first 20 cm of the tool gets incorporated.[9]

Although all of these experiments are fascinating (and in many cases extraordinarily ingenious), I will not detail them any further, mainly because body schema plasticity does not appear to be a distinctively human trait. That is, tool-using monkeys have also been shown to extend their body schema when using simple tools. The evidence in monkeys is in fact even more direct than in humans: Recordings of neuronal activity in Japanese macaques indicate that neurons originally picking out stimuli near the hand may, after just 5 minutes of tool use, come to respond to stimuli near the tool (Iriki et al. 1996).[10]

Of course, it still might be that humans outperform monkeys. For example, the capacity for tool assimilation might be inborn in humans, whereas a period of training might be needed to get it expressed in monkeys. In their review paper, Maravita and Iriki (2004) put forward this idea as a conjecture; but to the best of my knowledge, there is no direct evidence confirming it.

Summary: Body schema plasticity might be an important cognitive trait, even so important that without it, fluent tool use is not possible. We share the trait with our closest relatives, however. By implication, we cannot invoke it to explain what makes human technological abilities unique.

4. Causal reasoning

Causal understanding involves more than just noticing (e.g., through trial and error) the covariance between a cause (e.g., an action with a tool) and an effect (e.g., retrieval of a food item). One also needs to infer a mechanism relating the two – a causal relation explaining the occurrence of the covariance (e.g., Ahn et al. 1995; Ahn & Kalish 2000). Typically, such relations hold more generally than just in the context of discovery, and they can, therefore, once discovered, be exploited more widely. Knowledge that objects always fall under gravity, for example, is just as applicable to the manufacture and usage of deadfalls as of water butts and gallows. Are chimpanzees

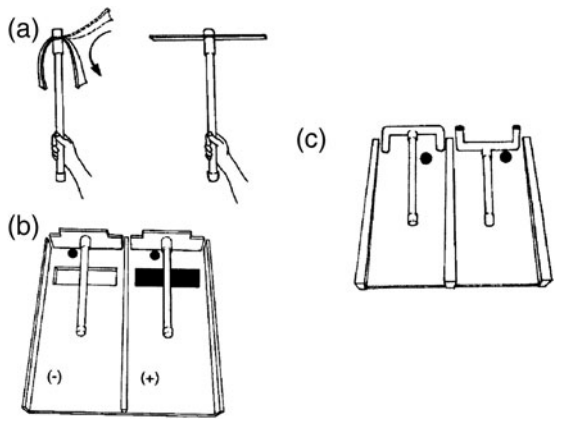

Figure 1. Three tasks used by Povinelli (2000) and colleagues to test causal reasoning in chimpanzees in the context of tool use. (a) The flimsy-tool problem, wherein chimpanzees had to choose between an ineffective rake (tines made of flimsy rubber) and an effective one (tines made of stiff tubing) to retrieve a food item. (b) The table-trap problem, in which the chimpanzees had to choose between pulling a rake that would cause the food item to fall into a trap (*left*) or one with which the food item could be successfully retrieved (*right*). (c) The inverted-rake problem, wherein chimpanzees had to choose between an upright rake and one that had been inverted, making the latter ineffective for food retrieval. (By permission of Oxford University Press, Inc.)

capable of discerning and flexibly putting to use such general causal principles?

Seminal experiments by Povinelli (2000) and colleagues suggest that they are not. In one of Povinelli's experiments, chimpanzees that were trained to use rakes for food retrieval failed to differentiate between functional rakes (made of stiff tubing) and nonfunctional ones (with their tops made of a thin strip of flimsy rubber) (see Fig. 1a). In another, the chimpanzees failed to appreciate that the food item would fall into a trap before being pulled to within reach (see Fig. 1b).[11] Finally, the animals failed to see that rakes with tines down were ineffective for capturing the reward (see Fig. 1c).

An important note: The chimpanzees could learn to avoid the causally unfavorable conditions. For example, after 25–125 (!) trials, all but one chimpanzee avoided the table-trap (in Fig. 1b). Hence, Povinelli's experiments suggest that chimpanzees learn about causality (or rather, about cause-effect covariances) through associative learning (dependent on contiguity and repetition) rather than through causal reasoning (i.e., inferring from the presence of a trap that the table containing the trap should be avoided).

Martin-Ordas and Call (2009) and Seed and colleagues (2009) qualified and refined these observations. Both groups of researchers found that chimpanzees could avoid (often already at the first trial) causally unfavorable conditions in tasks without tools, suggesting that the cognitive load associated with tool use is too high and blocks chimpanzees' ability to properly assess a task's causal set-up.

Furthermore, Martin-Ordas and colleagues (2008; 2009) examined the extent to which chimpanzees could transfer their causal knowledge across tasks. Their subjects consecutively completed different, but functionally equivalent trap tasks (involving a tube-trap, a table-trap, a platform-trap, and a gap-trap). It appeared that performances across tasks were not robustly correlated, which indicates that the apes did not make broad generalizations about the principles governing traps – an intuitive "trap physics" that can be applied to all kinds of traps.

Interestingly, transfer of causal knowledge across tasks plausibly depends on two related, yet distinct cognitive mechanisms.[12] The first is inferential causal reasoning: inferring the cause responsible for an observed cause-effect covariance (e.g., that this particular kind of trap causes food rewards to fall beyond reach). The second is analogical causal reasoning: appreciating that the causal principles governing this particular kind of trap are analogous to the principles governing other kinds of traps. Chimpanzees, the studies above suggest, face substantial difficulties in both inferential and analogical causal reasoning tests (although in the case of the former, only when tools are involved).

Humans, in contrast, are not just very proficient at, but, in fact, very fond of figuring out how things work.[13] From early on in their lives, they exhibit a remarkable drive for explanation (e.g., Gopnik 2000; Penn & Povinelli 2007a; Povinelli & Dunphy-Lelii 2001; Premack & Premack 1994; Visalberghi & Tomasello 1998). If a novel object behaves somewhat unexpectedly, for example, human children (from age 3 onward) seek causal explanations; whereas apes will explore the object in a way identical to that when exploring any other novel object they come across (Povinelli & Dunphy-Lelii 2001).

In many cases, humans establish causal inferences by diagnosing the unexpected outcomes of their goal-directed actions. Humans intervene nonrandomly in a situation to find out why anomalies occur; they run "tests" to confirm or disconfirm their initial hypotheses and updates thereof (Lagnado et al. 2007). Schulz and colleagues (2007) ran tests demonstrating that even preschool children (mean age: 56 months) can use information from interventions to distinguish between causal chains ($A \rightarrow B \rightarrow C$), common causes ($A \leftarrow B \rightarrow C$), and interactive causal structures ($A \leftarrow B \rightarrow C$ and $A \leftrightarrows C$). This kind of diagnostic learning is, in light of current scientific evidence, a uniquely human trait.

Intuitively, it is evident in what sense a grasp of causality has helped *Homo faber*. The more one knows about the causes of an event, the more likely that one can intervene and change the course of nature in one's own favor. Arguably, no light bulbs, phones, or spacecraft would exist without the causal relations established in science and engineering. For the moment, though, I leave the impact of causal reasoning on the evolution of human technologies intuitive, discussing it more fully in section 12.1.

What neural mechanisms are responsible for our capacity for causal reasoning in tool use contexts? In a short review, Frey (2003) remarks that neuroscience has largely ignored the question. The author mentions that to date there are some clues that processing of causal relations between self, tool, and goal object depends on higher-level temporal cortex, whereas the use of unfamiliar tools seems to involve parietal and/or joint parietotemporal mechanisms. On a more general level, for contexts without tools, Roser and colleagues (2005) found that causal inferential reasoning is likely left-lateralized. Analogical causal reasoning, by comparison, has not been studied as such. Inasmuch as it is a subtype of a more general capacity for analogical reasoning, research by

Morrison and colleagues (2004) suggests that it implicates brain regions related to working memory, inhibitory control, and semantic memory.

Summary: Causal thought involves both the ability to infer causal mechanisms relating cause-effect covariances (i.e., inferential causal reasoning) and the ability to recognize that such mechanisms underpin causally analogous events (i.e., analogical causal reasoning). Current evidence suggests that chimpanzees perform rather modestly in both respects. Humans, in contrast, have a drive for seeking and generalizing causal explanations, and often learn about causality through their own diagnostic interventions – a behavior not yet observed in the great apes.

5. Function representation

Primates do not attach particular functions to particular objects. For example, when trained to use a certain rake for food retrieval, a monkey will not stick to it when alternatives become available (e.g., Cummins-Sebree & Fragaszy 2005; Hauser 1997). The monkey switches opportunistically, using for food retrieval whatever it comes across. Likewise, there is no evidence for permanent function attribution in primates in the wild. After production and a one-time usage, chimpanzees typically discard their tools.[14] So instead of creating more permanent function-bearers, primates always manufacture tools anew and on the fly.

Humans, in contrast, use hammers for hammering, nutcrackers for nutcracking, cherry pitters for cherry pitting; and during their lifespan, these tools typically remain for what they originally were for. Once having conceptualized a tool as being for a particular purpose, humans find it even difficult to use a tool for something other than its designated function – a phenomenon called functional fixedness.[15]

A traditional explanation of this phenomenon relies on associative learning. Repeated exposure to a tool's design function causes motor programs associated with that function to be activated whenever the tool is encountered, blocking alternative, more creative uses (e.g., Kaplan & Simon 1990; Smith 1995). As chimps are capable of associative learning, the fact that functional fixedness occurs in us and (presumably) not in them just attests to our much more frequent engagement with technologies.

However, this traditional explanation has difficulties explaining the observation of Defeyter and German (2003) that functional fixedness in humans also occurs without repeated exposure to a tool. Being informed just once about a tool's conventional usage is sufficient to hinder non-conventional usage. From this, the authors infer the existence of a conceptual system – presumably unique to humans – for organizing and storing functional information.[16]

Additional evidence for such a conceptual system comes from neuropsychological observations of brain-injured patients suffering from apraxia – a disorder affecting the purposeful execution of learned behaviors.[17] Fluent tool use in apraxics may be disrupted in two ways: conceptual and motoric errors. In the case of conceptual errors, apraxics perform tool use actions skillfully, but out of context. A patient may, for example, eat with a toothbrush and brush his teeth with a spoon (Ochipa et al. 1992). So although the patient's relevant motor programs are intact, he is unable to associate them with the correct functions of toothbrush and spoon. Inversely, in the case of motoric errors, the patient knows about the function of a tool, but cannot activate the associated motor program to use it. For example, she may know that a spoon is for eating soup yet, when asked to use it for that purpose, grasp the spoon with the entire hand, instead of exhibiting the learned finger position associated with spoon use (Sirigu et al. 1995; also Buxbaum et al. 2003). In conclusion, fluent tool use relies on the intactness of two separate systems: (1) a conceptual system, which stores information about familiar tools and their usage; and (2) a production system, representing learned tool use skills.[18]

It is important to appreciate the relationship between functional knowledge and causal reasoning (as discussed in the previous section). Functional knowledge regulates usage of familiar tools (however causally opaque). If one encounters a familiar tool – say, a hammer – one can afford to stop reasoning about its possible uses and straightforwardly grasp it by its shaft. By so favoring a particular kind of usage, a functional representation may hinder causal assessments of situations in which the tool should be deployed in an atypical way (cf. functional fixedness). The point generalizes: Whenever conditions are unfamiliar (the tool or the task), the importance of causal reasoning increases.

Stable function representations plausibly facilitate ease of (re)use of a much wider diversity of specialized tools. Furthermore, given that it is general-purpose, functional knowledge may inform both tool production and usage, allowing alignment of the two in case they, as is common nowadays, are divorced.

Summary: There is converging evidence that human tool use depends on a conceptual system representing functional knowledge. Nonhuman primates, in contrast, do not attach particular functions to particular objects, which hinders (re)use of complex technologies.

6. Executive control

In outline, executive control refers to the voluntary control over actions. More specifically, executive systems subserve (1) inhibition, the capacity to suppress current drives (e.g., sex) for the attainment of long-term goals (e.g., a nulliparous life); (2) autocuing, the capacity to trigger certain behaviors autonomously; that is, in the absence of external stimuli (e.g., daily taking a contraceptive pill); (3) foresight, the capacity to form long-term goals (e.g., a nulliparous life), by prospecting needs other than those experienced in the immediate present; and (4) monitoring ongoing action, the capacity to monitor whether actions are indeed leading to the desired long-term goal (e.g., directing my attention to the contraceptives on the pharmacy shelf, away from distractors such as annoying background music).[19] Let me first consider how these four features bear on human tool use, and then assess the extent to which nonhuman primates display similar capacities.

According to Wynn (1981; 2002), monitoring ongoing action must have been present to allow for the emergence of Acheulean industries, some 1.5 million years ago. An exemplar of this industry is the Acheulean hand ax, which is produced by removing several flakes from a core so as

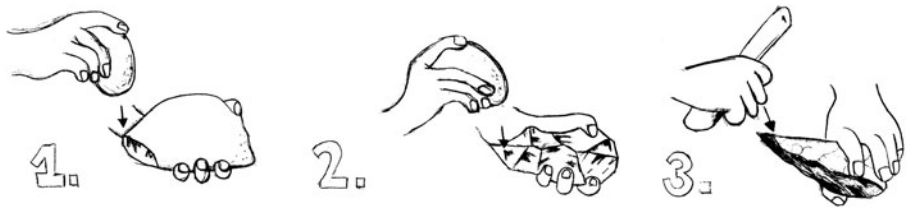

Figure 2. The production of an Acheulean hand ax. (1), (2) A hard hammer is used to achieve the basic shape of the ax by removing flakes from both sides of the core. (3) A soft hammer (made of bone, antler, or wood) is used to remove "thinning" flakes to achieve the final form of the ax. (Figure redrawn from Mithen 1996; courtesy of Lies Mertens.)

to yield a sharpened, standardized, teardrop shape (see Fig. 2). In a first stage, the basic shape of the tool is achieved by detaching flakes using a hammer stone. Next, the artifact is finished by using a soft hammer (from antler, wood, or bone). While removing the flakes, Wynn argues, early toolmakers needed to keep in mind the desired end shape and monitor whether flake removal properly affected the overall shape of the tool.

A recent neuro-imaging study by Stout and colleagues (2008) lends some support to Wynn's hypothesis. Stout and colleagues found that when modern humans, after the requisite training, engaged in Acheulean hand ax production, regions of ventrolateral prefrontal cortex were recruited. Increase of activation in these regions was observed during Acheulean-style, but not Oldowan-style, tool manufacture, reflecting the higher cognitive demands of the former. Importantly, these regions of prefrontal cortex are thought to indeed be involved in the coordination of ongoing hierarchical action sequences that are directed toward a higher-order goal (such as flake removal toward a standardized tool form).

Foresight (and inhibition; see below) is often linked to the advent of multi-component tools, such as the Levallois spears of 250,000 years ago (Coolidge & Wynn 2005; Wynn & Coolidge 2007). The thought is that intermediate goals (associated with each individual component) have to be brought into accord prospectively; the stone blade needs to fit the future wooden handle (or vice versa), and the binding material needs to fit both. One task (say, handle production) is put in abeyance (in working memory) until another (say, blade production) is completed (Aunger 2010).

If these sorts of multi-step action indeed depend on an ability for off-line planning, one can expect impairments of the human executive system to result in an inability to perform multi-step action. But that does not appear to hold unambiguously.

Goldenberg and colleagues (2007a), for example, studied multi-step action in patients with dysexecutive syndrome, involving the disruption of executive functions following damage to the frontal lobe. Dysexecutive patients may exhibit disinhibition of behavior (hence, produce inappropriate aggression, sexual behavior, and the like), attentional deficits, perseveration and utilization behavior, or lack of drive and initiative. The patients, when given the required items and a set of distractor items (teabags, a fork, and a bottle of milk), could take perfectly all steps needed to make coffee with a drip coffeemaker. So they managed to bring into alignment several items (water, water container, coffee, filter, coffeepot), each item having its own functional goal. Put differently, they managed to properly sequence actions with the relevant items, all to the attainment of an overall goal. The patients were able to "foresee," for example, that pouring in coffee before inserting a filter would not make the plan work.

On the other hand, the patients did perform poorly on two other multi-step action tasks. First, they failed on a pure problem-solving task (i.e., the Tower of London task; see Fig. 3) – where they had to work out a novel solution for themselves, rather than falling back on an established action routine (as in the coffee-making task). The default way of solving Tower of London problems is not through trial and error, but by mental planning ahead, indeed a capacity typically associated with executive function.

Second, patients faced substantial difficulties when asked to pack both a lunch box and a schoolbag with items specified by an instruction. Some of the items were lying on a table; others needed to be retrieved from a drawer, which also contained distractor items. The challenge was to keep both assignments in mind while switching between table and drawer, and while being distracted by unnecessary items such as toothbrushes and screwdrivers. Moreover, in contrast to the coffee-making assignment, the equipment here did not provide an external reminder of the goal of the task, so that the goal had to be maintained internally in working memory.

The upshot of Goldenberg's study is that executive functions are involved in preplanning innovative multi-step action and in monitoring ongoing action in the absence of external reminders, but not in the case of routine activities. Whether the advent of multi-component technologies really required a capacity for foresight, then, seems to

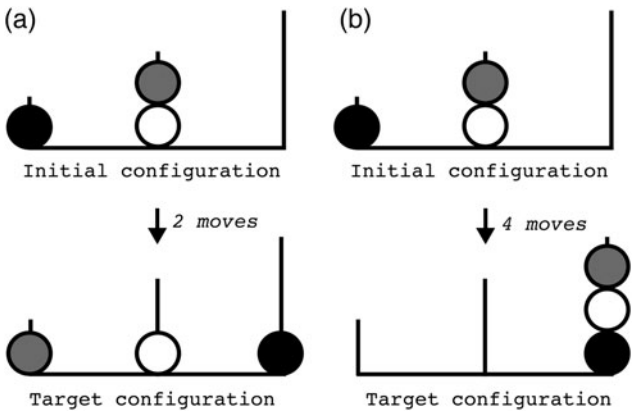

Figure 3. The Tower of London task: two initial configurations (a) and (b) with corresponding target configurations. Two moves are needed to get from initial configuration (a) to target configuration (a); four moves are needed to get from initial configuration (b) to target configuration (b).

depend on whether we conceive the event as one of innovation or of slow, haphazard adjustments to a set of established tool-making routines (more on this in sect. 12.2).

More convincing evidence of foresight are technologies such as traps and deadfalls. There one needs to predict how current actions will affect future events, without the environment providing immediate cues about how these events will unfold and without the environment serving as a reminder about which purposes the actions are supposed to serve (Coolidge & Wynn 2005). Unfortunately, traps and deadfalls do not preserve well in the archaeological record; some authors estimate their occurrence some 12,000 years ago (Bar-Yosef 2002; Moore et al. 2000; both cited in Coolidge & Wynn 2005).

Usually, planning ahead is successful on the condition that current drives are ignored. In trap building, for example, the delay in the reward is compensated for by the reward's higher nutritional value. So the trap-builder must inhibit actions on current appetite and postpone nourishment until the trap is filled. Likewise, in agriculture, it requires considerable inhibition to not consume the whole harvest, but save a portion for future planting instead (Coolidge & Wynn 2005). And finally, the more time and labor it costs to produce a certain tool, the more demands put on the inhibitory system (Coolidge & Wynn 2005).

According to Donald (1993; 1999), just as crucial as inhibition is its inverse: autocuing. Humans can "cue themselves" to act in certain ways, ways for which the environment does not provide any direct stimuli. Humans can voluntarily activate action schemes, for example, to engage in deliberate practice. Doing so leads to greater skill, which in turn allows for more complex tool use. Rossano (2003) conjectures that because skilled Acheulean toolmaking requires considerable practice, the Acheulean industry might provide us with the first evidence of an early form of autocuing.

How do apes fare with respect to (1) inhibition, (2) autocuing (3) foresight, and (4) monitoring ongoing action? To start with (2), autocuing has received little attention in the comparative psychology literature. None of the great apes has been reported to exhibit deliberate training in the wild, and no experiments have been conducted to test autocuing in captive nonhuman primates. So for now, we do not really know whether nonhuman primates can cue themselves to activate learned motor programs, offering them much broader windows of opportunity for improving skill.

Much more literature is available for (1), (3), and (4). Regarding (4), Stokes and Byrne (2001) have argued that chimpanzees engage in complex, flexible hierarchical action patterns, in a non–tool use context; namely, when processing leaves of the tree *Broussonettia papyrifera.* The authors document that while processing the foods, the chimpanzees need to monitor the progress they are making, as different intermediate results may require different types of follow-up action. The process is best represented by means of a standard decision tree, with multiple pathways and loops leading to and serving the overall goal (viz., processed food). In a tool use context, Boesch and colleagues (2009) have observed something similar: They found that chimpanzees used five different objects – in the correct functional order – to obtain honey.

Quite a few studies have recently attempted to find evidence for (1) and (3). The study coming closest to proving something like inhibition and foresight is by Osvath and Osvath (2008).[20] The authors report on two chimpanzees and an orangutan that seemed to select a tool (viz., a drinking straw) to retrieve a larger delayed reward (half a liter of highly favored fruit soup), instead of selecting an instant smaller reward (a grape). But, as Suddendorf and Corballis (2009) remark, because the apes went through a substantial training phase, the results can still be explained in terms of simple associative learning, with the apes' repeated experience with straw and fruit soup forging a strong connection between the two. What is more, Suddendorf and Corballis (2009; also, e.g., 1997; 2007) rightly point out that human foresight and inhibition are not just a matter of "sitting out" a current desire, biting the bullet until satiation; human forethought also involves foreseeing and acting on a future drive, which might be qualitatively different from current ones (e.g., not drinking too much wine now, to be fit tomorrow). Because grapes and fruit soup tap the same desire (viz., hunger), Osvath and Osvath's study – supposing for a moment that associative learning can be excluded – gives at best evidence of apes being in control of a current drive, not of planning a future one.

In fact, to have current and future goals diverge, one must be able to entertain more than two qualitatively different goals to begin with. Although chimpanzees certainly have more than one drive (food, mating, shelter, territorial protection), it is uncontroversial that the range of goals that chimps pursue pales in comparison with the range of human goals (e.g., Csibra & Gergely 2007; McGrew 1993). Humans even may take as a goal the satisfaction of someone else's anticipated goals – as happens when one individual produces a tool for another (often thereby tapping theory of mind abilities; see sect. 9).

Summary: Executive control is the capacity for (1) inhibition; (2) autocuing; (3) foresight; and (4) monitoring hierarchically structured, ongoing action. Comparative evidence for (2) is lacking; humans and chimpanzees both seem to perform well on (4). In light of current evidence, however, humans still appear to have unique abilities for (1) and (3).

7. Social learning

In 1987, Tomasello and colleagues observed that chimps were able to learn from a model that a T-shaped rake affords food retrieval, yet ignored the exact way in which the model operated the rake. Tomasello (1990) took this to be the characteristic difference in social learning between apes and humans. Apes are capable of emulation, reproducing the goal achieved by the model; humans, in contrast, are imitators, copying not just goals, but also the means towards them.

Tomasello's proposal remains controversial (although it is often presented as settled). The most systematic challenge comes from a series of experiments conducted by Whiten and colleagues, three of which are particularly forceful.

First, Whiten and colleagues (2005; also Horner et al. 2006; Whiten et al. 2007) showed that chimpanzees can sustain technologies within the population through mechanisms of social transmission.[21] For example, Whiten et al.

(2005; 2007) experimentally introduced two different foraging techniques into two different captive groups, by training one individual of each group then reintroducing it to its respective group. Under the influence of their local expert, most chimpanzees adopted the method seeded in their group. Moreover, even if a chimpanzee individually learned the alternative foraging technique, it nevertheless continued to deploy the technique used by most of its peers; as such, conforming to the cultural norm of the group.

If emulation is default among chimpanzees, and they learn about results (emulation) rather than about actions (imitation), one could expect them to be able to learn also in the absence of action-information. In a second study, Whiten and colleagues (Hopper et al. 2007) tested this hypothesis using ghost conditions; that is, conditions in which the tool task was not demonstrated by a model, but rather was performed automatically/mechanically. If environmental effects are sufficient to learn about a task, then chimpanzees should be able to perform the task also after having been exposed to the ghost condition. This, however, was not observed. Chimpanzees appeared not to learn in the ghost condition, although they got skilled after having observed another chimpanzee performing the task. This suggests that the model's actions are needed for transmission to ensue.

In a third study, Horner and Whiten (2005) found that chimpanzees are able to switch between emulative and imitative strategies. When causal information regarding the operation of a tool remains opaque, chimpanzees tend to imitate, as well as copy the causally irrelevant actions performed by the model. When this causal information becomes available, though, they emulate, omitting causally irrelevant behaviors, individually devising a suitable – and more straightforward – method to attain the goal attained by the model.

In light of these studies, Tomasello (2009) has recently qualified his original position. He grants that apes indeed appear responsive to both goals and means. Nonetheless, Tomasello (also Whiten and colleagues, for that matter) still notes remarkable differences between chimps and humans, be it in degree rather than in kind. He rightly notes, for example, that Horner and Whiten's observation of imitation/emulation switching in chimpanzees contrasts starkly with their observations in human infants. In particular, Horner and Whiten (2005) report that infants imitate in the causally opaque condition (like the chimps), but also in the causally transparent condition (unlike the chimps). So even when given information about the irrelevance of an action, human infants copy it; as such, engaging in what is often called overimitation (e.g., Hernik & Csibra 2009; Lyons et al. 2007; McGuigan et al. 2007; Whiten et al. 2009). Given their relative ignorance, it apparently pays children to faithfully copy by default, correcting errors later in life, once they are capable of reading the minds of models (see sect. 9), of being receptive to instruction, and/or of understanding the causal structure of tool use tasks.[22]

Two other features are characteristic of human social learning – although they are more intuitive than corroborated experimentally. First, humans can socially acquire not just means, but also a remarkably wide variety of nonbasic goals; that is, goals that are not directly linked to drives such as food and sex and shelter (piety, a healthy old age, a unique collection of stamps).[23] Social learning in chimps, in contrast, is typically triggered by the prospect of one of the not-too-distant goals in the ape's innate goal repertoire – usually a food reward. At present, there is little evidence suggesting that chimps can extend that repertoire by copying parts of someone else's.

Second, humans are not just better imitators, they plausibly are better at emulating, too.[24] As long as problems are not too complex, a chimp may try-and-err its way to an emulated goal state. Higher complexity, however, increases the range of possibilities for reaching the goal, making random trial and error ineffective. Humans are fairly good emulators also in these circumstances. For many of us, for example, the default way of learning how to put to use new and complex electronic devices is through emulation. Instead of carefully carrying out all steps described in the manual, we are able to infer proper usage from function – perhaps because our grasp of causality constrains the range of possible actions we consider and try out or because we notice analogies with the usage of other devices (see also sect. 12.1).

Summary: Human social learning is special in three respects. First, humans start as faithful, nonselective, default imitators, developing more selective modes of imitation over the years. Second, humans commonly acquire through social learning not just means, but also a remarkably wide variety of nonbasic goals. Third, emulation learning, too, is plausibly much more powerful in humans than in the great apes.

8. Teaching

Social learning can moreover be facilitated by a trait not so much of the imitator as of the model being imitated. More specifically, learning proceeds more smoothly if the model has the willingness and a capacity to teach. For example, if the model actively shows which actions are relevant and which ones can safely be ignored, the imitator does not need a causal grasp of the situation to be successful. The imitator may be ignorant because she is too young, or because the ultimate causal effects of the action are opaque. For example, as Csibra and Gergely (2006; 2009) point out, if there is a divorce between the production and use of a tool, as in making a tool for a tool, there are no perceptual rewards that can be used as immediate clues concerning the relevance of certain actions.[25] From your observation today of someone affixing a spear point to a shaft by means of a rope, you cannot infer the action's relevance for killing a boar tomorrow. In such circumstances, it helps if the model assists you; for example, by emphasizing salient actions through repetition, by pointing to the functional features of a tool, by contrasting proper versus improper usage, and so forth.

For teaching, language is helpful but not requisite. Before mastering a language, human infants learn a lot by relying on nonverbal cues (e.g., of their parents): simple gestures such as pointing or showing objects; sounds of excitement or disapproval in case of success or failure; looking for eye contact, gaze shifting and capturing, or redirecting attention (Csibra & Gergely 2006; 2009).

By and large, it is agreed that such active pedagogy is uniquely human, notwithstanding two isolated

observations of (supposed) teaching in chimpanzees by Boesch (1991).[26] To be sure, it is common that mother chimpanzees stimulate their offspring to engage in tool use (e.g., by leaving stones and nuts in the vicinity of the anvil), and even facilitate it (e.g., by lending their own preferred tools to their infants); but active teaching is extremely (!) rare, if existent at all.[27]

Summary: Human teaching is unique: Until now, no nonhuman species has been reported to engage systematically in the kind of active teaching commonly observed in *Homo sapiens*.

9. Social intelligence

Here I discuss four profound dependencies between sociality and tool use: (1) heuristics for selecting models for social learning; (2) theory of mind abilities; (3) contingent reciprocity; and (4) goal sharing.

Let us start with the first. To avoid adoption of maladaptive behavior, social learners should be capable of selecting as models those individuals that possess adaptive information. Humans deploy several heuristics to that end. These fall into two categories: model-based and frequency-dependent heuristics.[28]

In the former, particular features of the model are used to estimate the potential benefits of social learning. As a copier, one might preferentially select particularly successful individuals (inferred from their previous successes); particularly prestigious individuals (inferred from the amount of deference shown to them by other individuals); or individuals that are simply similar to oneself (inferred from self- and other-recognition; similarity can work on different criteria, such as similar age, similar ethnicity, similar dialect, etc.). In all three cases, social cues are used to select individuals worth learning from.

The cues of single individuals still might be ambiguous. So a second set of strategies – namely, frequency-dependent strategies – exploits information aggregated over the behavior of many individuals. If most of one's group members do *X*, chances are high that doing *X* pays off, given that selective forces are at work in each individual of the population. The inverse of this conformity bias may also occur; namely, when the rarity of a behavior is used as a cue.

No such biases have been observed in great ape social learning.[29] But that both types of model selection are potent mechanisms for technological innovation is uncontroversial: If individuals in a population are able to select and learn from the most skilled individuals, *ceteris paribus*, the average skill level of the population increases – stated otherwise, the population as a whole innovates.

Let us turn to the second sociocognitive trait facilitating tool use: understanding the mental life of others. Thirty years of research have not solved Premack and Woodruff's (1978) question of whether chimpanzees have a theory of mind. According to Povinelli and colleagues (Penn & Povinelli 2007b; Povinelli & Vonk 2003), on the one hand, evidence is still lacking for something remotely resembling chimp mental state attribution. According to Call and Tomasello (2008), on the other, chimpanzees have in several experiments displayed at least some grasp of the mental life of others. Notwithstanding that fact, Call and Tomasello, too, believe that chimpanzees lack the full-fledged belief-desire psychology of humans.

Theory of mind abilities interact with human tool use in at least two ways (both hinted at already). First, social learning of complex tool-using and tool-making activities is facilitated when the learner understands the model's intentions – that is, the model's motives for executing some actions yet omitting others (e.g., Cheney & Seyfarth 1990; Tomasello 2000). Theory of mind is one of the plausible mechanisms involved in the transition from overimitation to selective imitation. Second, theory of mind makes possible the divorce of tool production and usage. Making a tool for someone else is contingent on the recognition that the other may need the tool in question. Contemporary market research is a good exemplar of how theory of mind abilities may drive technological change.

The third dependency between sociality and tool use concerns contingent reciprocity and the way in which it supports strong divisions of labor, at both kin and nonkin levels. At kin level, a remarkable feature of humans is their sexual division of labor. In hunter-gatherers, for example, one sex is specialized in gathering, the other in hunting, and the revenues of both are shared to the benefit of the entire household (Marlowe 2007). Such division of labor yields a broader and more reliable diet and an increase of skill level, which in turn leads to greater foraging success rates.[30] In chimpanzees, in contrast, males and females target different foods but do not share revenues within the sexual pair bond.

The point, in fact, generalizes: Chimpanzees are reluctant to exchange foodstuffs. Plant food sharing has been observed only sporadically outside the mother-infant dyad.[31] Male hunting chimpanzees do share meat with non-kin; but this usually evidences mutualism (in this case, male allies are given their share; see below) or one-time pay-for-sex strategies (i.e., swollen females receive a chop), not specialization or division of labor (e.g., Stanford 2001; Stanford et al. 1994).

Moreover, these redistributions are very local, and involve only those group members present at the kill. Bipedalism means that humans can transport gathered foodstuffs and carcasses, allowing them to develop much wider exchange networks.[32] Also, transportation of food to more permanent dwellings enables delay of consumption. And when foods can be stored, it starts to pay off to specialize in food production, because excesses can be saved for future consumption or future exchange.

Quadrupedal chimpanzees face severe limitations in this sense: Investments in specialization (say, the production of sophisticated weaponry or other tools) can be brought in balance only with immediate rewards – that is, immediate consumption or immediate exchange (followed by immediate consumption of the exchanged goods). To make it even worse, chimpanzees also face a cognitive handicap: Their limited sense of contingent reciprocity precludes the development of reliable exchange networks.

Contingent reciprocity occurs when A's helping of B is contingent on B's previous help toA.[33] Stevens and Hauser (2004) discern seven cognitive requirements for contingent reciprocity (see Table 1). I have already discussed two of them (i.e., time estimation and temporal discounting) in section 6 (both under the heading of

Table 1. *Cognitive requirements for contingent reciprocity*

Time estimation	See section 6
Cheater detection	?
Punishment	?
Reputation recognition	?
Temporal discounting	See section 6
Numerical discrimination	Hanus & Call 2007; Tomonaga 2008
Memory	de Waal 1989; Matsuzawa 2001 But see Brosnan et al. 2009; Melis et al. 2008
Empathy	de Waal 2006; Warneken & Tomasello 2006 But see Jensen et al. 2006; Silk et al. 2005

Note: The second column gives references to reports describing absence/presence of these requirements in chimpanzees. The symbol "?" indicates that no systematic data are available.

inhibitory control). For three of them (i.e., cheater detection, punishment, and reputation recognition), there is little to no evidence in nonhuman primates. The last two are borderline cases: numerical discrimination and memory. Numerical discrimination – necessary to make exchanges equitable, for if absent, defectors give back less than a fair amount – has been observed in all of the great apes (e.g., Hanus & Call 2007; Tomonaga 2008).[34] Regarding memory: Although chimpanzees do have reliable memories of past interactions with others when it concerns services such as grooming or support (especially de Waal 1989; also de Waal 2000; Matsuzawa 2001), such mental score keeping has not been observed when it concerns exchanging foods for foods (Brosnan et al. 2009; Melis et al. 2008). Finally, Table 1 contains an eighth cognitive trait, not mentioned by Stevens and Hauser (2004), but proposed by Brosnan and Beran (2009) – namely, empathy. The idea is that reciprocal exchange is facilitated by an ability to recognize someone else's needs, and a willingness to act thereupon. Although such other-regarding behavior has been reported in chimpanzees, again it does not come off in food contexts.[35]

To sum up, expensive investments in tool use will pay off if one can share or exchange outputs exceeding one's own consumption. That, in turn, requires sophisticated mechanisms for contingent reciprocity. When limited in this sense, as is the case with chimps, strong divisions of labor and highly specialized toolkits are unlikely to evolve.

The fourth and final relation between social intellect and tool use regards goal sharing – that is, many individuals aligning their goals so as to produce group beneficial outputs. Many authors invoke such a form of mutualism to characterize some of the oldest tools found in the archaeological record. Toth and Schick (2009), for example, conjecture that Oldowan tool production was a social enterprise, with production sites being used by large social groups. Acheulean hand axes presumably required even more social organization. These axes were – at least according to some – thrown to knock down animals, after which a group of hunters could club the animal (Calvin 1990).

But even if Acheulean hand axes testify to a quite sophisticated social intellect, they do not yet indicate any superiority over nonhuman primates. After all, chimpanzees, just like humans, strongly cooperate while foraging for meat (but, unlike humans, typically go hunting unarmed) (e.g., Boesch 1994; 2002; Boesch & Boesch 1989). The most salient difference in social behavior between chimp and human contemporary meat foraging is, according to Stanford (2001), that humans (unlike chimps) coordinate hunts with vocal and gestural communication. Therefore, to the extent that prehistoric hunters can be modeled on contemporary hunter-gatherers, it would be more natural to argue that cooperative hunting depends on improved communicative abilities, rather than on goal sharing per se.

Better evidence for increased demands on social intelligence would come from technologies that are produced by many individuals, or from technologies the use of which is unequivocally more socially involving. One contender is the colonization of Sahul (or Pleistocene Australia–New Guinea) some 45,000 years ago. That event arguably required cooperation in production and usage, of marine modes of transportation in particular. Another contender is the decorative use of beads (110 kya), implying early modes of communication and perhaps even trade. It also might be that the first multi-component tools already marked a difference in sociality. That is, it might be that the first hafted tools (250–200 kya) were produced by many – each individual responsible for (or even specialized in) the production of one component, complementing one another to achieve a common goal. Indeed, the attainment of that particular common goal would strongly depend on a careful coordination between team members.

Summary: Four sociocognitive traits in particular are to the advantage of *Homo faber*: (1) recognition and assessment of social cues as a proxy for a model's copy-worthiness; (2) theory of mind abilities, facilitating selective social learning and the divorce of production and usage; (3) strong forms of contingent reciprocity, which enable profound divisions of labor and specialization; and (4) goal sharing, which helps to distribute the costs of complex technologies among collectives of individuals. Our nearest relatives score (much) lower in all four domains.

10. Language

There are some obvious ways in which language facilitates advanced tool use: Thanks to language, processes of social learning and teaching and cooperation proceed far more efficiently; technological knowledge is more easily preserved in linguiform format and therefore can accumulate over longer periods of time, distributed over larger groups of individuals; linguistic and other representational artifacts (from symbol systems, sketches and books to computers and models) speed up the cognitive process of technological innovation; language paves the way for more symbolic forms of cultural behavior.

Yet, it is far from certain that language was necessary to make human technologies diverge from those used by our closest relatives some 2–3 million years ago.[36] On the contrary, numerous scholars have argued exactly the opposite: Early advances in human tool use played a causal role in

the evolution of language. It is this point, rather than the more mundane contribution of language to modern tool use, that is widely investigated and debated. This section sketches the contours of the debate.

Roughly, there are two plausible ways of spelling out the evolutionary transition from tool use to language. Sequence A is as follows (e.g., Arbib 2005; Bradshaw & Nettleton 1982; Corballis 2010; Gibson 1993; Stokoe 2001): (1) Advanced tool use gave good control of arm and hand; (2) such manual dexterity automatically made for increased gestural capacity; that is, it was exapted for communicative purposes; (3) a similar form of fine control was later applied to oral movements, leading to speech.[37]

Arbib (2005) remarks that tool use actually offers an excellent opportunity for the kind of gestural communication implied in step 2: When teaching an infant to use a tool, pantomiming becomes salient (also Rizzolatti & Arbib 1998). While the infant holds the tool, the model acts out what the infant is supposed to do. In the pantomime, the model performs an action that is instrumental in origin, but communicative in the context of teaching. That is, the resources needed to perform the instrumental act can be simply recruited to engage in communication – it "just" requires a slightly different mind-set.

Sequence A is mainly inferred from observations of patients with local left-hemispheric brain lesions, which at the same time affect linguistic, gestural, and object-manipulation capacities. Patients suffering from aphasia, for example, often fail to perform easy actions with tools, such as unlocking and opening a door (e.g., Kimura 1979); and defective pantomiming (e.g., of tool use) is almost always associated with language deficits such as aphasia.[38]

However, the finding that regions for language and tool use overlap does not suffice to justify the particular chronology suggested by sequence A. For that, one needs to make an extra assumption; namely, that gestural communication indeed preceded vocal communication. It is a plausible assumption to the extent that one believes that our closest relatives exhibit greater gestural than vocal capacities; for under that condition, our common ancestor must also have possessed better gestural than vocal skill.

The second way of spelling out the transition from tool use to language draws on the exaptation not so much of fine motor control as of resources for processing complex hierarchical structures (e.g., Bradshaw & Nettleton 1982; Gibson 1990; Greenfield 1991; Higuchi et al. 2009). Version B of the causal-temporal sequence, then, is as follows: (1) Advanced tool use gave humans the capacity to combine and integrate lower-order elements (viz., actions) into higher-order units; (2) resources initially devoted to structuring manual hierarchies were exapted for linguistic purposes (viz., for combining phonemes into words, words into meaningful sentences, and so forth).

Section 6 already discussed (B1). I showed there that Acheulean toolmaking requires the ability to organize and execute a sequence of manual operations (viz., different sorts of flake removal) in such an order that a higher-level goal is achieved (viz., a standardized hand ax). Put differently, the overall action (viz., Acheulean toolmaking) consists of an ordered set of subactions. A similar hierarchical organization is observed in human languages. Sentences consist of lower-level units such as clauses, which also consist of lower-level units such as phrases, words, and eventually, phonemes.

What (B2) suggests, now, is not just an analogy between the organizations of tool use and language but a common origin (with the hierarchical organization of tool use evolving first). Evidence for (B2) comes from three quarters: developmental studies and lesion and neuro-imaging studies.

With respect to the first, Greenfield (1978; 1991) observes remarkable parallels in the development of skills for organizing manual actions and words. For example, children start to be able to pair objects (e.g., putting a smaller cup in a bigger cup) around the same time that they learn how to pair words. In a similar vein, but somewhat later, they develop strategies to combine more than two objects (e.g., putting a cup in a cup, both of which are then put in a third, even bigger cup) around the same time at which they learn how to nest words into sentence-like structures.

For a proof of common origin, concurrent development is insufficient, though. It still might be that both types of organizational skills develop in parallel coincidentally and are regulated by two separate neurological structures. Now lesion studies – the second type of evidence for B2 – complement the developmental data in support of a common origin. Grossman (1980; reviewed by Greenfield in Walker 2009), for example, reports on agrammatic patients with Broca's aphasia. These patients lack hierarchical organization in their syntactic production; they just sequence individual words, without relating them so as to produce meaningful overarching structures (phrases, clauses, sentences). Grossman found that Broca's aphasics also face substantial difficulties when reproducing hierarchically ordered drawings, such as tree structures (like those used to represent genealogies or phylogenies). He concludes the existence of a domain-general hierarchical processor, which can be used to organize both basic linguistic and nonlinguistic elements into complex constructs.

Finally, neuro-imaging studies in support of (B2) point to the recruitment of particular regions in Broca's area during both tool use and linguistic tasks. Higuchi and colleagues (2009), for example, found increased activation in Brodmann's area BA44 when subjects manipulated common tools (scissors, pencils, and chopsticks) and when they were listening to a narrator reading a Japanese fairy tale. The perception of the hierarchical structure of a set of utterances (as in the fairy tale comprehension task) therefore appears to be regulated by the same neural resources governing the hierarchical organization of manual movements.

Moreover, Higuchi and colleagues (2009) make plausible on neurological grounds that computational principles for processing complex hierarchical structure originally evolved to support tool use and were exapted for grammatical purposes later. Because F5, the region in the monkey brain thought to be homologous to BA44, is involved in tool use just as well, and because monkeys lack syntactically structured language, it is reasonable to think that only humans have put to use their capacity for hierarchical organization (subserved by BA44) outside the domain of its origin.

As a final remark, it is noteworthy that sequences A and B are not mutually exclusive. On the contrary, it is likely that tool use has given rise both to fine gestural/oral

control and to a capacity for hierarchical organization. Of course, even if this is right, an important question remains; namely, whether these two abilities coevolved (i.e., A and B happening concurrently) or one of them evolved first, thereby, perhaps, triggering the emergence of the other.

Summary: Although language has contributed enormously to the sophistication of human technologies, the prehistoric divergence between humans and other primates with respect to tool use is most likely not attributable to linguistic ability. On the contrary, accumulating evidence suggests that human tool use has played a causal role in the evolution of human language, rather than the other way around. Still, many of the details of the causal pathway from tool use to language remain uncertain.

11. Overview

Let me briefly summarize my findings up until here. My comparison has revealed striking differences between humans and great apes – roughly, for eight of the nine cognitive domains discussed (for a more detailed and balanced assessment, see the overview in Table 2). Humans benefit from, roughly, better hand-eye coordination (sect. 2); a unique system for causal thought (sect. 4); a unique system for representing functional knowledge (sect. 5); remarkable inhibitory control and foresight (sect. 6); a suite of sophisticated social learning strategies (sect. 7); a unique disposition for teaching (sect. 8); increased social intelligence (sect. 9); and all the fruits of language (easing social learning and teaching, knowledge preservation, cooperation, innovation, and the like; sect. 10).

Apparently, therefore, human tool use attests to a major cognitive discontinuity between us and our closest relatives. And relatedly, apparently no individual cognitive trait can be singled out as the key trait differentiating humans from other animals. In other words, my overview should be an antidote to single-trait explanations of "humaniqueness."

Bearing this in mind, I now turn to the second part of the paper. I consider how the cognitive traits discussed add up, producing the technological complexity characteristic of our lineage.

Table 2. *Cognitive capacities subserving complex tool use.*

Hand-eye coordination	
Higher-order visual analysis	+
Fine motor control	++
Population-level handedness	+
Body schema plasticity	=
Causal reasoning	
Inferential causal reasoning	++
Analogical causal reasoning	++(?)
Diagnostic learning	++(?)
Function representation	++
Executive control	
Inhibition	++
Autocuing	?
Foresight	++
Monitoring hierarchical action	=(?)
Social learning	
Imitation	+/++
Emulation	++(?)
Social acquisition of goals	++(?)
Teaching	++
Social intelligence	
Model selection	++(?)
Theory of mind	+/++
Contingent reciprocity	
Time estimation	++
Cheater detection	++(?)
Punishment	++(?)
Reputation recognition	++(?)
Numerical discrimination	+/++
Memory	+/++
Empathy	+/++
Goal sharing	+/++
Language	++

Note: The symbol "++" indicates that the trait is highly more pronounced in humans than in chimpanzees. The symbol " + " indicates that the trait is more pronounced in humans. The symbol " = " indicates similar capacities in humans and in chimpanzees. The symbol "?" implies that little comparative evidence is available. Symbols are attributed in light of current scientific evidence; more detailed explanations are given in the text.

12. Cumulative culture and the complexity of human technologies

The complexity of human technologies is tightly linked to our remarkable ability for cumulative culture: Humans have been able to build complex systems by accumulating modifications over successive generations, gradually improving on previous achievements.[39]

Key in recent explanations of this phenomenon is high-fidelity cultural transmission: Accumulation will take place when innovations are passed on to subsequent generations without degenerating too much (e.g., Boyd & Richerson 1985; 1996; Henrich 2004; Henrich & McElreath 2003; Richerson & Boyd 2005; Tennie et al. 2009; Tomasello et al. 1993). The thought is intuitive, but not without problems.

First, there is the classic problem of the Acheulean. The continuity of Acheulean hand axes on vast scales of time (1 million years) and space (from Africa to India to Wales) must have been sustained by very accurate mechanisms of cultural transmission (e.g., Lycett & Gowlett 2008; Mithen 1996; 1999; Petraglia et al. 2005; Shipton 2010; Toth & Schick 1993). Yet, there is no clear sense in which later generations of Acheulean assemblages built further on previous ones; first signs of genuinely cumulative culture are found in much more recent times, with, for example, gradual refinements of prepared-core and multi-component technologies. In light of this, it is reasonable to suppose that cumulation requires more than high-fidelity transmission alone.

Second, even if one grants that high-fidelity transmission is just a necessary condition for cumulative

culture, the question remains of how it is implemented. Most seem to agree that sophisticated mechanisms for social learning and active teaching are essential.[40] However, these labels also black-box much of the cognitive machinery implied. The research described in section 7, for example, suggests that human infants copy more faithfully than chimpanzees do when it concerns relatively simple tasks, such as retrieving food from a box by means of a stick. But it is doubtful that this basic, and apparently fairly blind, disposition neatly scales up to learning much more intricate behaviors of the kind needed for sustaining incrementally complex technologies. Rather, it is more likely that other cognitive capacities need to be added; for example, that causal thought is part and parcel of human social learning, and hence, of high-fidelity cultural transmission.

These two issues are addressed below. I reconsider four cognitive traits that do not directly link to high-fidelity cultural transmission and show how: (1) by improving individual learning, they may complement processes of high-fidelity transmission (accommodating the insufficiency objection); (2) by facilitating social learning and/or teaching, they may subserve high-fidelity transmission (accommodating the black-box objection). Because at various points my arguments remain speculative, I also identify a set of issues in need of empirical validation.

The four traits in question are causal reasoning (as discussed in sect. 4), executive control (as discussed in sect. 6), and the capacities for contingent reciprocity and for goal sharing (both discussed in sect. 9).[41]

12.1. Causal reasoning and cumulative culture

Boyd and Richerson (1995) point out that social learning is adaptive when social learning makes individual learning more effective; in particular, if it allows individuals to learn selectively: individually, if cheap and accurate; socially, if individual learning is difficult and error-prone. By implication, for cumulation to take place, individual learning costs must remain low. If not, all will switch to social learning – everyone imitating everyone – with cultural stasis or decline as a result.

Consider now the assumption that individual learning costs increase proportionally to the complexity of technologies. Indeed, labor-intensive technologies quite plausibly raise the costs of, for example, individual random trial-and-error learning. Whereas a one-minute experiment (say, in Oldowan flake production) may be excusable, executing month-long random trials (say, in boat production) is a cost that no single individual should be willing to bear. Likewise, the causal structure of a technology can be so intricate that the likelihood of success of a random adjustment approaches nil. So even if an individual is prepared to spend her valuable resources on arbitrary interventions, her result will almost always be inferior to that obtained through social learning. Eventually, that strategy is the one she adopts, and cumulation comes to a halt.

So if I am right, the accumulation of complexity is constrained by the cost-effectiveness of individual learning strategies.[42] At some level of complexity, more sophistication in individual (rather than social) learning is required to produce further complexity.

How can, in the face of accruing complexity, the cost of individual learning be reduced? A capacity for causal reasoning helps, for it makes individual learning targeted. Causal thought allows individuals to consider and learn directly about the salient features of a problem, not wasting resources on the limitless array of irrelevant factors. Suppose a particular deadfall is effective for catching small amphibians (e.g., frogs). One can easily learn how to apply the deadfall to larger animals (e.g., rabbits) – if one appreciates that it is the deadfall's dimensions and bait, rather than its operational principles, that are in need of experimentation. Rather than random and difficult, individual learning gets targeted and affordable.

Even if early technologies owed little to scientific theory, and they are consistent with being the product of trial and error, the kind of trial and error involved was plausibly reasoned rather than random: Given a folk understanding of the reasons for success or failure of an action, some interventions were tried, but not others. Causes inferred from diagnostic learning and causal analogies (e.g., that hafts are useful not just for spades, but also for rakes and hoes) were brought to bear in order to structure and delineate ill-structured design problems and spaces. This happened even more so towards the late 18th century, when science really began to have an influence on technology (although it is true that science is not a good example of strict individual learning; but more on this in sect. 12.3) (Mokyr 2002; Wolpert 2003).

We do not know whether by boosting individual learning, an improved grasp of causality forced the deadlock of the Acheulean. For what it is worth, by the time cumulative culture really got off the ground (say, in the Middle Stone Age), human brain size had increased substantially (e.g., Rightmire 2004). Yet, whether this improved our causal reasoning capacities is uncertain, especially given our uncertainties regarding the neural mechanisms underlying causal thought (see my discussion in sect. 4).

Fortunately, my argument is general enough not to suffer from our ignorance about the precise whenabouts of the evolution of causal thought. If increased complexity indeed discourages individual learning, and a capacity for causal thought can ease the burden of such learning, then causal thought (whenever it emerged) is a plausible explanans for why cumulative culture evolved so markedly in humans and so modestly in apes.

Apart from reducing individual learning costs, causal reasoning abilities may also positively affect social learning. In particular, causal reasoning may facilitate: emulation learning (e.g., when putting to use a new device without consulting the user's manual, or when reverse-engineering)[43]; selective imitation (i.e., copying only causally salient actions) (e.g., Want & Harris 2001); and proper model selection (e.g., copy X's doing of Y, because X's success is attributable to her doing of Y).

12.1.1. Outstanding questions.

1. Almost all studies concerning inferential causal reasoning, analogical causal reasoning, and diagnostic learning use only Westerners as human subjects.[44] Are these forms of causal thought universal and observable cross-culturally?

2. Can the intuitive link between causal thought and individual inventiveness be empirically validated?

3. Although inferential causal reasoning in chimpanzees has received considerable attention, how do chimpanzees fare with respect to analogical causal reasoning and (especially) diagnostic learning?

4. To what extent does causal thought smooth social learning – in any of the three ways described above?

12.2. Executive control and cumulative culture

Improved executive control may positively affect cumulative culture in four ways. First, it may facilitate social learning. On this hypothesis, social learning of complex action sequences requires extra resources for representing interactions with the model; the social learner must inhibit her current drives longer, pay attention to the model's relevant behaviors only, and put into accord various actions (past, current, and future) of both model and herself.[45] To the best of my knowledge, no one has systematically addressed the impact of executive functions on social learning.

Second, improved executive functions may contribute to cumulative culture by lowering the costs of individual learning. The study of Goldenberg and colleagues (2007a; discussed in sect. 6) lends some support to this thought, for the authors show that dysexecutive patients perform poorly on innovative tasks, such as Tower of London tasks. For this sort of problem solving, Goldenberg and colleagues argue, it is apparently necessary to mentally plan ahead the steps to take. On this account, executive control would lower individual learning costs in largely the same way as causal reasoning does: by making individual learning reasoned rather than random. Innovation is easy for farsighted individuals, cumbersome for the arbitrary trial-and-error learner.

Third, better executive control may allow the representation of increasingly complex behaviors (however learned). But, as explained in section 6, this idea is questioned by the finding of Goldenberg and colleagues (2007a) that dysexecutive patients are able to execute quite complex routine action sequences (such as making coffee with a drip coffeemaker). Perhaps even more complex routine tasks put higher demands on executive functions; those not involving external reminders are likely to. At any rate, the relationship between executive control and complex action representation, however intuitive, has not been established yet.[46]

Fourth, inhibition of immediate drives makes room for other motives, and those are remarkably diverse in humans. Two nonbasic motivations in particular can be expected to act on cumulative culture: the motivation to be like others, and conversely, the motivation to be unlike others (better than, different from). These act in opposite directions: the former furthering conformity and preservation of traits, the latter promoting competition and the introduction of new cultural variants. The former has been claimed to be characteristic of small-scale egalitarian societies (or of humanity, even) (e.g., Henrich & McElreath 2003); the latter is usually associated with modern cultures valuing personal achievement and the strive for excellence (e.g., McClelland 1985). The speed of technological progress in capitalist societies since the Industrial Revolution seems to indeed be correlated with motivations to excel and outperform others. True, the rapid spread of many of our inventions may well attest to strong norms of conformity; their enormous diversity is more consistent with pronounced motivations not to be like others.

Incidentally, as was the case for causal thought, it is unknown whether improved executive functions, in any of the four ways described above, were implied in the Acheulean–Middle Stone Age transition.

12.2.1. Outstanding questions.

1. Does social learning of complex behaviors really increase the demands on executive functions? (For example, does dysexecutive syndrome affect social learning?)

2. Goal maintenance and planning ahead appear to be critical for innovative tasks, such as solving Tower of London problems. Does the same hold for other innovative acts, especially those involving tools?

3. Models of cultural evolution have largely ignored the effects of nonconformity.[47] Questions related to nonconformity include: How do individual achievement motives favor individual learning? Increase variation? Speed up innovation rates? How does the resulting competition affect cumulation?[48]

12.3. Social intelligence and cumulative culture

Section 9 discussed four sociocognitive skills: (1) heuristics for assessing a model's imitation-worthiness; (2) theory of mind abilities; (3) strong forms of contingent reciprocity; and (4) goal sharing. Cultural evolution theory has amply discussed the effects on cumulative culture of the former two. In this section, I consider the role of the latter two.

12.3.1. Contingent reciprocity. Contingent reciprocity supports cumulative culture, first, by allowing nonvertical modes of social learning and, second (again), by lowering individual learning costs.

First, when active teaching is involved, nonvertical modes of social learning are more difficult to establish than are vertical transmission modes. As teachers have no genetic interest in helping non-kin apprentices, their help is dependent on other forms of return on investment. These may be indirect (e.g., increasing the teacher's prestige) or direct (e.g., receiving favors from the apprentice or apprentice's close kin). In the case of the latter, mechanisms for contingent reciprocity seem crucial.

There is much discussion about how important nonvertical modes of transmission have been in initiating human cumulative culture.[49] On the other hand, the role of oblique and horizontal transmission in sustaining cumulative processes, especially in the modern era, is undeniable.[50] Equally undeniable is the role of contingent reciprocity in it – teaching has become an economic good, just like butter and bread.

Second, the effect of contingent reciprocity on individual learning relates to the fact that contingent reciprocity supports strong divisions of labor, also when learning is concerned. Consider, for example, a subsistence farmer who tries to learn individually which crop to plant.[51] The crop's eventual yield is dependent on numerous factors (e.g., climatic variations, soil conditions, pests), not just crop choice; so the farmer would need to experiment quite a bit before knowing which crop truly is best. Because she is unlikely to be willing to bear the costs of these experiments alone, she can be expected to just

plant whatever crop other farmers plant(ed). Other farmers, too, will prefer social learning over individual efforts, and cumulation will come to a halt.

The stalemate can be broken if the farmer's learning costs are distributed: that is, if the farmer spends her resources on optimizing crop choice while others carry out the remaining tasks in return. The farmer specializes in farming, others in weaving rugs, baking pottery, grinding flour, and so forth. Goods are exchanged, and cumulation occurs in all domains. Unlike causal thought and executive control, contingent reciprocity thus lowers individual learning costs relatively rather than absolutely: Instead of making individual learning less laborious, contingent reciprocity ensures the labor of learning does not preclude the satisfaction of the other necessities of life.

There are some intuitive interconnections between contingent reciprocity, on the one hand, and causal thought and executive control, on the other. Contingent reciprocity makes teaching profitable. The effect of teaching on cumulative culture, in turn, can be expected to increase if the teaching not only transmits certain domain-specific skills (as in traditional transmissions of crafts), but also promotes capacities for individual learning (e.g., by passing on domain-general causal knowledge; see sect. 12.1) and motivates learners to put these capacities to use (e.g., by insisting on virtues of personal achievement and, popular since the Enlightenment, of thinking for oneself; see sect. 12.2). These reinforcement relations, however, still lack empirical and/or model-theoretic bite.

12.3.2. Goal sharing. Individual learning costs can be distributed in yet another way: by, as it were, making individual learning social. Now several individuals bundle their efforts to produce group-beneficial learning outputs. Cognitively speaking, the individuals display goal sharing in a learning context.

Several farmers, for example, may invest in a small, collective experimental patch of land where they can try out different crop varieties. The outcome of these experiments is to the benefit of the collective; each group member can now plant the crop the group jointly has identified as best.

At a certain level of behavioral complexity, individual specialization insufficiently reduces individual learning costs, and joint learning strategies (of the sort just described) need to arise for adding further complexity. Take, for example, the fairly modest transition from CD to DVD technologies. Even this small incremental improvement was initially the product of a joint effort of four major electronics corporations. Later, the technology was developed further by an even much larger consortium, the DVD Forum, consisting of 195 member companies in 2007. In other words, no single individual could have invented the DVD, even if, as cultural evolution theorists are fond of stressing, much of the work had been already done by previous generations.

As said (see Note 50), we don't know whether the evolution of nonvertical modes of transmission terminated the Lower Paleolithic, nor whether the evolution of joint learning had anything to do with it.

12.3.3. Outstanding questions

1. What are the conditions under which costly, nonvertical modes of teaching evolve? Which of the cognitive presuppositions of contingent reciprocity (see Table 1) can be expected to be crucial?

2. Cultural evolution theory has studied the preconditions, interactions, and effects of individual and social learning. What are the preconditions and effects of joint learning strategies, and their interactions with individual and social learning strategies?[52]

13. Conclusion

Only human animals have been able to produce complex technologies such as wireless communication networks, satellite-driven navigation systems, and devices for arthroscopic and nanobot surgery. I have shown that this remarkable feature reflects a profound discontinuity between us and nonhuman primates in matters of social and non-social intelligence. And I have explained, albeit tentatively, in what sense our social and non-social cognitive sophistication has contributed to the technological accumulation characteristic of our species.

ACKNOWLEDGMENTS

Research by Krist Vaesen was supported by the Netherlands Organization for Scientific Research (NWO). He would like to thank six anonymous reviewers, Alex Mesoudi, Wybo Houkes, Marieke van Holland, and Auke Pols for useful comments on previous versions of this text.

NOTES

1. For reasons of space, and because tool use has been studied in primates more extensively than in other species, the contrast class for humans will be chimpanzees (and on some occasions, the broader class of primates). I agree that future research should determine whether similar conclusions can be drawn for, for example, crows, finches, dolphins, otters, and elephants. Furthermore, my list of cognitive traits reflects my individual judgment and discretion. My selection was mainly guided by research in the cognitive sciences: Only traits that received marked attention there made it to the list. Although my overview may not be exhaustive, I believe it is fairly representative for what we currently know about the cognitive bases of tool use.

2. Several authors have claimed to have found the humanique trait. For an elegant overview, plus forceful counterargument, see Penn et al. (2008).

3. Some believe that the inability of Kanzi (the world-star bonobo; see Toth & Schick 1993) to produce proper Oldowan flakes proves enhanced hand-eye coordination in humans. I think that the experiments on Kanzi prove very little: first, because of the peculiar incentive structure of the experiments; and second, because simple biomechanical explanations may suffice to explain its underperformance.

4. Some methodological concerns: (1) The study of Orban et al. (2006) was conducted on rhesus monkeys, not chimpanzees; (2) the study of Stout and Chaminade (2007) was conducted (evidently) on modern humans, so inferences about the role of dorsal IPS in early tool users should be made with care.

5. Population-level right-hand biases have been reported in the wild for, for example, drinking water and nutcracking (Biro et al. 2006), termite fishing (Lonsdorf & Hopkins 2005), and ant dipping and extraction of palm heart (Humle & Matsuzawa 2009).

6. See the meta-analysis performed by Hopkins (2006).

7. Here is how Head and Holmes put it, as early as 1911: "Anything which participates in the conscious movement of our bodies is added to the model of ourselves and becomes part of

those schemata: a woman's power of localization may extend to the feather of her hat."

8. For (1): see, for example, Maravita et al. (2002). For (2): see, for example, Berti and Frassinetti (2000). For (3): see, for example, Farnè and Làdavas (2000) and Maravita et al. (2001). For an overview, see Maravita and Iriki (2004).

9. For a similar point, relying on a different kind of experiment, see Holmes et al. (2004).

10. For a study showing profound similarities between human and chimpanzee tool integration, see Povinelli et al. (2010).

11. The use of traps to test for animal causal knowledge was introduced first by Visalberghi and Limongelli (1994).

12. This is observed both by Martin-Ordas and colleagues (Martin-Ordas et al. 2008; Martin-Ordas and Call 2009) and by Penn and Povinelli (2007a).

13. For a recent overview of the literature, see Keil (2011).

14. See, for example, Boesch and Boesch (1984) and McGrew (1992); for a rare report of tool reuse, see Carvalho et al. (2009). Hunt (2006) observes a link between chimpanzee quadrupedalism and the limited complexity and durability of chimp tools. Because chimpanzees feed arboreally and, when on the ground, use their hands to walk, they have difficulties carrying both the tools they previously made and the excess in foodstuffs resulting from their tool use. In light of this, investments in complex and durable tools simply do not pay off.

15. The phenomenon was first described by Duncker (1945). Evidence for the universality of the trait is presented by German and Barrett (2005).

16. For the uniqueness of the trait, see also Casler and Kelemen (2005).

17. For a useful overview, see Frey (2004).

18. For neurological evidence, again see Frey (2004); for a recent follow-up study, see Goldenberg and Spatt (2009). The sizable literature on function representation contrasts with how little is known about the storage of learned behaviors, such as tool use skills (Frey 2007). The existence of such a production-level storage system in humans and other primates is indubitable; what remains uncertain, however, is in which respects (if at all) the human production-level system differs from that of nonhuman primates. To be clear, the question is not whether humans acquire many more technical skills than nonhuman primates do, because that fact is trivially true. Rather, the question is whether our large skill repertoire really requires extra cognitive/neural innovations; perhaps having a larger brain simply suffices (Gibson 2007).

19. On many an occasion, inhibition, autocuing, foresight, and monitoring ongoing action overlap. For example, when acting on a plan for the long-term future (foresight), I often suppress actions on current needs (inhibition) while keeping track of the things that I am actually doing to bring the future state about (monitoring). For present purposes, however, the four categories are convenient to be used to structure the wide variety of studies and hypotheses concerning executive control and human tool use.

20. Other primate studies concerning forethought include Mulcahy and Call (2006b) and Naqshbandi and Roberts (2006). For planning in birds, see Raby et al. (2007).

21. For an earlier suggestion of imitation among chimpanzees, see Whiten et al. (1996).

22. The precise developmental trajectory of selective imitation remains unclear. Some suggest selectivity already around the age of 14 months (see, e.g., Gergely et al. 2002); others suggest that infants do not imitate (let alone, selectively) until their second year (e.g., Jones 2007; for a useful overview, see Jones 2009).

23. For a similar suggestion, see, for example, Csibra and Gergely (2007) and McGrew (1993).

24. Laland and Hoppitt (2003) briefly consider the possibility that emulation rather than imitation is the default means of information transmission in humans.

25. A similar suggestion is made by Aunger (2010).

26. Boesch reports two independent, unreplicated cases of a mother chimpanzee demonstrating the use of a stone for cracking a nut. For a set of alternative interpretations of Boesch's observations, see Tomasello (1994).

27. For a description of stimulation and facilitation in chimpanzees, again see Boesch (1991).

28. See the overview by Henrich and McElreath (2003). For a review of empirical research on model selection heuristics, see Mesoudi (2009).

29. Two exceptions may seem Horner et al. (2010) and Whiten et al. (2005). Yet, these studies define conformity and prestige differently to how Boyd, Richerson, and Henrich define them. Whiten et al. (2005) define conformity as simply doing what other group members are doing; whereas Boyd, Richerson, and Henrich define it as being disproportionately more likely to copy the most common behavior (compared with copying at random). Horner et al. (2010) equate "prestige" with dominance; whereas Henrich and Gil-White (2001) make a clear distinction between prestige and dominance, the latter based on ability to coerce and fight (found in many species), the former based on deference and knowledge (found only in humans).

30. An alternative interpretation is that men engage in hunting for other, less noble reasons – that is, they hunt to signal their quality to potential mates. Marlowe's cross-cultural study, however, contradicts this interpretation.

31. Two reports of wild fruit sharing are Nakamura and Itoh (2001) and Slocombe and Newton-Fisher (2005). Hockings et al. (2007) conjecture that lack of wild fruit sharing does not reflect a lack of willingness to share, but rather the fact that the wild fruits that chimpanzees harvest are too small to be shared. The authors base their hypothesis on the observation that chimpanzees share more when large cultivated fruits are available. For sharing plant foods in captivity, see, for example, de Waal (1989).

32. In *The Descent of Man*, Darwin already remarked on the importance of bipedalism in the explanation of human distinctness. But, to be clear, bipedalism appeared some $3\frac{1}{2}$ million years before the first stone tools. Hence, bipedalism is at best a necessary condition for complex tool use.

33. In addition to contingent reciprocity, de Waal (2000) discerns two lower forms of reciprocity: symmetry-based reciprocity (based on symmetries inherent to dyadic relationships; e.g., kinship) and attitudinal reciprocity (reciprocating positive attitudes, without exact accounting of favors given and received). These have been documented among chimpanzees (for an overview, see Brosnan & de Waal 2002); whereas evidence for contingent reciprocity in chimpanzees remains scarce. For early, theoretical treatments of contingent reciprocity (labeled "direct reciprocity" there), see Axelrod and Hamilton (1981) and Trivers (1971). Direct reciprocity contrasts most naturally with indirect reciprocity; for example, A helping B because of B's reputation to be generally helpful to others (Nowak & Sigmund 2005).

34. For a review of symbolic numerical competences in chimpanzees, see Matsuzawa (2009).

35. For evidence of other-regarding behavior in chimps, see, for example, de Waal (2006) and Warneken and Tomasello (2006). For absence of other-regarding behavior in food contexts in chimps: see, for example, Jensen et al. (2006) and Silk et al. (2005). See also the discussion on teaching, in section 8.

36. I here just assume, uncontroversially, a vast discrepancy between human and chimp linguistic abilities. For an insightful overview, see Premack (2004).

37. Calvin (1993) explains why it is not strange to think that the neural machinery for moving the hand may affect capacities to move the mouth. Although it is true that hand and mouth are represented in different compartments of the motor cortex, fine control is more a matter of preparing movements in the premotor and prefrontal cortex. Fine motor control, in other words,

is more domain-general (i.e., applicable to hand and mouth) than the prima facie independence of hand and mouth might suggest.

38. For an overview, see Kempler (1993). For more recent treatments, see Goldenberg et al. (2007b) and Króliczak and Frey (2009).

39. Even though cumulation has been observed in nonhuman species, it remains fairly modest (see Whiten et al. 2003 for a detailed overview).

40. Social learning and teaching, in turn, are likely facilitated by bipedalism and good hand-eye coordination (see sect. 2).

41. I leave out theory of mind and language in my discussion not because I think they are unimportant, but because their importance has been claimed by so numerous authors before. Instead, I focus on traits the impact of which is less debated but, as I hope to show, far-reaching nonetheless.

42. For a similar observation, including empirical and model-theoretic support, see Mesoudi (2011). His and my observations are similar to, yet different from, those of McElreath (2010). McElreath suggests that individual learning must be sufficiently developed to get cumulation started. Mesoudi and I suggest a further step: Once started, the cumulative process will come to a halt without further investments in individual learning.

43. Experiments by Caldwell and Millen (2008) indicate, tentatively, that cumulative effects may also occur in humans when they are given opportunities for emulation only. Caldwell and Millen simulated generational succession by repeatedly removing and replacing participants while giving them simple tasks, such as building paper planes. Planes of later generations flew significantly farther than those constructed by earlier generations, even if participants could learn through emulation only; that is, by being given the opportunity to inspect just the planes, not the actions of their makers.

44. This is, in fact, a general shortcoming of studies in the behavioral sciences, as Henrich et al. (2010) point out. Exploratory papers concerning causal thought across cultures are Lewis (1995), Morris et al. (1995), and Norenzayan and Nisbett (2000).

45. Of course, similar requirements could hold for those individuals involved in active teaching.

46. Incidentally, conceptual systems such as those discussed in section 5 may also be involved in more complex action representations. The functional information stored there provides a shortcut to proper usage; coffeepot, filter, water container, and so forth, can be put to use forthwith, without prior trial-and-error investigation.

47. The existence (rather than the effects) of conformity and nonconformity biases has been studied fairly extensively; for a useful overview, see Mesoudi (2009). For the idea that conformity is not default in social learning, see, for example, Efferson et al. (2008) and Mesoudi (2011).

48. Attempts to model competition between cultural variants are found in evolutionary economics; see, for example, Saviotti (1996) and Saviotti and Metcalfe (1984).

49. There seems to be considerable agreement that vertical transmission dominated the Acheulean (see, e.g., Mithen 1994; Shennan & Steele 1999; but see Lycett & Gowlett 2008). Much more disagreement exists about what happened next. Richerson and Boyd (2005; 2008) believe that nonvertical transmission evolved towards the end of the Pliocene; Shennan and Steele (1999) argue that for complex skills, such as tool-related crafts, vertical transmission has remained dominant, likely until the modern era.

50. This is consistent with models of Henrich's showing that complex skills may get lost if populations display low social interconnectedness – for example, when individuals learn only from their parents (Henrich 2009). If populations are highly interconnected, inventions spread more widely, and as such, are better secured against loss through inaccurate transmission or accidental loss of the best models in the population. Notably, the more complex the skill in question, the more interconnectedness is needed to sustain and improve it. Henrich (2004; 2009) also shows that population size matters; a similar result is obtained by Powell et al. (2009). These arguments, however, should not be interpreted as showing that population size alone is sufficient for cumulative culture, for they presuppose mechanisms of nonvertical transmission. So population size can have its effect on the condition that certain cognitive capacities (such as contingent reciprocity) are in place.

51. The example is drawn from Henrich (2002) and Sterelny (2006).

52. Work in evolutionary economics and organization theory may serve as a source of inspiration here. For a useful review covering relevant findings in both fields of study, see Dodgson (1993).

Open Peer Commentary

Tool use and constructions

doi:10.1017/S0140525X11002123

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Abstract: We examine tool use in relation to the capacity of animals for construction, contrasting tools and nests; place human tool use in a more general problem-solving context, revisiting the body schema in the process; and relate the evolution of language and of tool use.

Tools versus nests. Many creatures can use tools *of a specific kind*, and in some cases, even make them, as do New Caledonian crows (Hunt 1996; Weir et al. 2002). Lefebvre et al. (2002) conclude that the complex cognitive processes involved in tool use may have independently co-evolved with large brains in several orders of corvine and passerine birds. Nonetheless, it seems to me that nest building by birds is even more impressive than their tool making is; and indeed, Hansell & Ruxton (2008) urge that we view tool behaviors as a limited subclass of construction behavior. Nest building in birds has been a key driver of habitat diversification and speciation in these groups (Collias 1997; Hansell 2000). It is therefore intriguing that Stewart et al. (2011) show that re-use of specific nest sites by savanna chimpanzees may be a result of "niche construction" (Iriki & Taoka (2012) Laland et al. 2000) through formation of good building sites within trees. They speculate that environmental modification through construction behavior may have influenced both chimpanzee and early hominin ranging by leaving behind recognizable patterns of artifact deposition across the landscape.

Human tool use in construction. Let us shift attention from "using a tool" to the ability to deploy multiple tools to solve a problem. To join a piece of wood to the wall, I may employ a screw of sufficient length plus a screwdriver or a nail and hammer. I may also employ a stud finder, but if I need to affix an object where there is no stud, I deploy a rawlplug, a drill, and a hammer to prepare for the screw. For household repair, I may deploy these tools and more to solve a truly novel

problem by breaking it down into subproblems for which I have routine solutions. Or I may call in a handyman, thanks to the great specialization within human society and the social construction of monetary incentives.

An etymological detour to the *Oxford English Dictionary*: The word *handiwork* ("a thing made by the hands") comes from the Old English *hand* + *geweorc*. As *geweorc* ≈ *iwork* did not survive in Middle English, *hand-iwerc* was reanalyzed as a compound of *werc* with *handi*. *Handi* was eventually treated as an adjective, *handy*, meaning "of, or done by, the hand" when used in new compounds – including *handy-man*. The point here is that the refined shape and controllability of the human hand must be complemented by many changes in the brain to yield "handyness." Of the nine cognitive capacities listed by Vaesen, only three – enhanced hand-eye coordination, body schema plasticity, and function representation – relate directly to using a tool for its intended purpose. Two – causal reasoning and executive control – relate not so much to tool use as to the more general skill of problem solving (of which construction, with or without tool use, is a crucial subcase). The remainder – social learning, teaching, social intelligence, and language – all relate to social interaction in general or the transfer of skills in particular, whether or not they involve tool use.

Vaesen argues that only one of these nine capacities, body schema plasticity, cannot be invoked to explain what makes human technological abilities unique as "we share the trait with our closest relatives." However, the issue is not whether the body schema can be extended, possibly by extensive shaping as in monkeys (Iriki et al. 1996; Umiltà et al. 2008). Rather it is (in part) the uniquely human rapidity and flexibility with which different extensions of the body schema can be deployed in some overall task, switching back and forth between using some part of the body or some part of a tool as the end-effector for the current action (Arbib et al. 2009).

Language. Vaesen distinguishes two routes from tool use to language:

> Advanced tool use promoted manual dexterity that was exapted for communicative purposes; a similar form of fine control was later applied to oral movements, leading to speech.

> Advanced tool use gave humans the capacity to combine and integrate lower-order actions into higher-order units; resources initially devoted to structuring manual hierarchies were exapted for linguistic purposes.

and cites the mirror system hypothesis (Arbib 2005) as an example of the former. However, the actual theory overlaps both and makes no appeal to *advanced* tool use. Rather, it stresses *complex imitation*, the ability to recognize and imitate combinations of actions used to reach a perceived goal, together with variations on known actions. Recently, inspired by Stout's (2011) essay on stone toolmaking and the evolution of human culture and cognition, I developed a scenario (still in rather rudimentary form) in which complex imitation underwrites the co-evolution of language and toolmaking, with neither required to reach a critical complexity to initiate the evolution of the other (Arbib 2011; a somewhat modified account appears in Arbib 2012). In this regard, it is useful to think of the grammar of a language not as a very general set of syntactic rules but rather as involving a large number of constructions that provide tools for assembling words hierarchically to meet the communicative goals of both familiar and novel social situations (Arbib & Lee 2008; Croft 2001; Goldberg 2003; Kemmerer 2006; Verhagen 2005).

Conclusion. Vaesen closes his article by saying that he has "explained, albeit tentatively, in what sense our social and non-social cognitive sophistication has contributed to the technological accumulation characteristic of our species" (sect. 13). Notably, the direction here – from social and non-social cognitive sophistication to technological accumulation – does not privilege tool use as the driver for human exceptionalism, and therefore challenges us in our evolutionary thinking to consider the diverse interactions that must have driven the evolution of these capacities singly and in tandem.

Evidence of recursion in tool use

doi:10.1017/S0140525X11001865

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Abstract: We discuss the discovery of technologies involving knotted netting, such as textiles, basketry, and cordage, in the Upper Paleolithic. This evidence, in our view, suggests a new way of connecting toolmaking and syntactic structure in human evolution, because these technologies already exhibit an "infinite use of finite means," which we take to constitute the key transition to human cognition.

In section 10 of the target article, Vaesen reviews some of the approaches that link increased complexity in tool use to language evolution. For example, several proposals have seen in the mode of production of Oldowan choppers (2.6 mya) and/or Acheulean hand axes (1.7 mya) the kind of structural complexity that characterizes human language: that the kind of finer motor control involved in tool use facilitated speech control (Calvin 1993); or that hand motor control for tool use was rather instrumental in the appearance of a gestural mode of communication that is supposed to predate oral language (Arbib 2005; Rizzolatti & Arbib 1998); and that such tools illustrate the kind of hierarchical structure that is characteristic of language (Greenfield 1991).

These approaches take for granted an early scenario for language evolution; that is, that the structural capacity required for grammar is already present in the abilities manifested in early hominin tools. Late scenarios for language evolution, on the contrary, contend that language is connected to the transition to Homo sapiens and its diaspora from Africa, which started about 120,000 years ago. In other words, it is in the behavioral complexity and cultural explosion of the past 100,000 years of human evolution where the critical changes that account for human uniqueness are to be looked for. In so doing, a stronger evolutionary discontinuity is established between human and non-human primates. Given Vaesen's concern in the target paper to argue for a cognitive discontinuity between human and non-human primate tool use, he should be sympathetic to such late scenarios and pay attention to the structural complexity involved in the tools of this age, rather than just the early ones he discusses.

It is from this standpoint that Upper Paleolithic knotting technologies (Adovasio et al. 1996; Sofer et al. 2000) are relevant in this context. Knotting technologies are involved in basketry, nets, and textile weaving. Archeological remains of such crafts consist of clay imprints, dated circa 30,000 years ago. Binding by knotting can also be inferred in the case of spears, harpoons, and arrow heads and their corresponding bows (c. 70,000 years ago), which had to be strongly attached to their shafts (older spears were glued to their bases; see Wadley 2005). Perforated ornaments, such as necklaces, bracelets, and wristbands, also were tied. Two features of these tools need to be underlined: They appear just in the last 70,000 years, and they are associated with Homo *sapiens* sites (ornaments also appear in late Neanderthal sites in Europe, but after they got in contact with the newly arrived *H. sapiens*).

It has been suggested (Camps & Uriagereka 2006) that the formal structure of knotting is similar in complexity to a context-sensitive grammar, such as that required to capture recursivity in human language. Relying on Chomsky's (1959) formal hierarchy, Camps and Uriagereka claim that knots also could involve a context-sensitive generative procedure. They observe that the procedure for tying a knot cannot be specified as an iterative sequence of steps (a finite automata), because

each step in the procedure has to have access to previous stages and the material context of physical forces the knot is made to resist. The kernel of their reasoning is the claim that the knotting procedure involves higher-level units ("phrases"), which are deployed according to the material context. This is obvious when one thinks of the sophisticated ways of sailor knots. In general, though, the two hands have to mutually coordinate along the procedure, rather than doing one thing after another. Context sensitivity is linked to operational memory requirements, to keep track of each operation, taking the previous and next ones into account at the same time. From this, Camps and Uriagereka claim that the archeological evidence of knots – even if indirect and inferential – provides the best indication available of a cognitive complexity equivalent to that required by human language.

We think that their case can be strengthened in two directions: First, whereas in projectiles and perforated ornaments a single knot may be required to fix two elements together or to string them around the body, in textiles, nets, and basketry a series of knots is involved, within a general constructive plan (therefore, a more complex, context-sensitive, generative procedure). Second, such a series of knots is in the service of recursive patterns, which can be transformed, following distinct axes of symmetry, for example. Simple iterative processes are clearly not enough to generate such complex structures, where each single operation is conditional on the state of the rest of the fabric and the physical forces the knot is supposed to resist.

Besides, knotting cannot be accounted for in terms of Greenfield's "action grammar," which is equivalent to a finite-state automata. She contented that the structural complexity of language can be also found in hierarchical organization of action. The kinds of actions she paid attention to, though, such as "Russian dolls" inclusion, are developmentally easier than knot tying is, and they are also within the reach of non-human primates (whereas knots are beyond the capacities of chimpanzees, according to Josep Call, personal communication). Therefore, the attempt to view recursion in terms of Greenfield's "action grammar," as it has been recently suggested (Fujita 2009), does not pay proper attention to the context sensitivity of recursion.

On the other hand, the proposed connection between knotting and language entails that the program proposed by Hauser et al. (2002) got it right that recursion is uniquely human, but wrong that it is a uniquely linguistic capacity, even if the evidence is still not enough to decide how it came about: It could be a general capacity, deployed in different domains, or a domain-specific one that was exapted in others (Barceló-Coblijn, in press). It also offers a plausible hypothesis to set apart the linguistic capacities of *sapiens* and *neanderthal*, given that both species cannot be distinguished at the speech level (Barceló-Coblijn 2011). In summary, context-sensitive rules offer a principled mark of modern humanity, beyond the typical lists of modern behaviors that can be found in archeology (Henshilwood & Marean 2003).

Tool innovation may be a critical limiting step for the establishment of a rich tool-using culture: A perspective from child development

doi:10.1017/S0140525X11001877

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Abstract: Recent data show that human children (up to 8 years old) perform poorly when required to innovate tools. Our tool-rich culture may be more reliant on social learning and more limited by domain-general constraints such as ill-structured problem solving than otherwise thought.

Vaesen is right to identify the tension between the need for reliable conservation of tool forms and the need for deviation from reliable reproduction if new tools are to be created. Yet, he does not draw a clear enough distinction between the cognitive demands of tool *innovation* and other aspects of tool use. Tool innovation is seen when individuals make a tool to solve a problem without learning socially or having seen a model solution. Where Vaesen refers to human children's tool use, it is to emphasise human beings' strengths from a very early age (e.g., sect. 4). However, taking a developmental perspective on human tool use has shown that tool innovation may be particularly difficult for human children, compared with using pre-made tools. Successful innovation in older children and adults is needed to explain the unique richness of human tool culture, whereas the difficulty of innovation observed in human children casts new light on the importance of other abilities, such as social learning, for retaining hard-won innovations.

We (Beck et al. 2011) tested human children on a tool making task based on Weir et al.'s (2002) wire bending problem. This task was originally made famous by the successes of a New Caledonian crow (*Corvus moneduloides*) and more recently rooks (*Corvus frugilegus*) (Bird & Emery 2009). Having previously used a hook to retrieve a bucket from a tall vertical tube, these corvids were then able to fashion a straight piece of wire into a hook to solve the task: that is, they used novel means to make a familiar tool. We questioned whether children would innovate a novel tool, critically without having seen the solution to the task (a hook).

Children up to 5 years old found it near impossible to innovate a novel tool to solve this task, and it was not until 8 years of age that the majority of children succeeded (Beck et al. 2011). Children's difficulty was replicated on a task requiring them to unbend a bent wire to make a long, straight tool (Cutting et al. 2011) and on tool-innovation tasks involving other materials and other transformations (i.e., adding and subtracting from the tool object as well as bending; Cutting et al., under review). The results could not be attributed to a lack of causal understanding: Young children readily used a pre-made hook tool to solve the vertical tube task (Beck et al. 2011, Experiment 1). Nor could results be explained by a pragmatic resistance to adapting the materials: Children's difficulties remained in the face of ample encouragement to reshape the wire (a pipe cleaner). We gave children pre-trial experience manipulating the materials, encouraged them to "make something," and demonstrated tool manufacture on a different task (see Cutting et al. 2011).

Children's ability to select an appropriate pre-made tool indicates that they did not lack the causal knowledge to solve the task (in Vaesen's terms, *analogical causal reasoning*; see sect. 4). Furthermore, when an adult demonstrated how to make an appropriate tool, almost all children (97%) found it apparently trivially easy to *manufacture* their own tool and fish the bucket from the tube (Beck et al. 2011). Why, then, is tool *innovation* so late developing?

One possibility is that an over-reliance on social learning and/or teaching (see sects. 7 and 8) prevents children from innovating for themselves. We agree with Vaesen that human children are experts at learning from others. But a species that evolves to pass on information so efficiently to new learners does so at a cost. It is inefficient and possibly counterproductive for children to try to generate their own solutions to problems as well as adopt them from others. At least in childhood, if not also in adult life, the ability to innovate may be sidelined in preference to learning from the more experienced individuals who share our goals and are motivated to collaborate with us (see sect. 9).

However, we doubt that this will be the full explanation. Vaesen argues that developing an advanced technological

culture requires trial-and-error learning and causal understanding. In addition, we suggest that tool innovation is challenging because it makes distinctive demands on executive function. In cognitive and neuropsychological investigation of executive function, "ill-structured" problems are tasks that do not exhaustively define the means of getting from the start point to the goal, but instead require participants to generate such structure for themselves (Goel 1995). From this perspective, tool innovation is clearly an intrinsically "ill-structured" problem: Participants know the goal (e.g., of retrieving the bucket from the tube), and their start point includes the necessary materials (e.g., the wire), but they must generate for themselves the strategy of using the materials to make the necessary tool. As ill-structured problem solving has been associated with late-maturing areas of medial prefrontal cortex (Dumontheil et al. 2008), it is likely to be limited in young children. Hence, unlike trial-and-error learning and causal understanding, which may be observed in young children, difficulty with ill-structured problem solving may explain why children find tool innovation so surprisingly difficult.

Recognising that tool innovation might be an intrinsically difficult problem helps us understand why the capacity for social learning is so important for the development and maintenance of a tool-using culture in both humans and non-human animals: Social learning avoids individuals having to "reinvent the wheel" for themselves. Furthermore, if tool innovation requires ill-structured problem solving, this might help explain why tool cultures of non-human animals are less rich than those of humans. Importantly, though, this leaves open the question of how non-human animals develop the tools that they have. One possibility is that they rely only on trial and error, the useful products of which are maintained through social learning. Another possibility is that tool cognition provides a window onto non-human animals' ill-structured problem solving, through which we might gain important understanding about the origins of executive control.

Tool use as situated cognition

doi:10.1017/S0140525X11002147

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Abstract: Vaesen disregards a plausible alternative to his position, and so fails to offer a compelling argument for unique cognitive mechanisms. We suggest an ecological alternative, according to which divergent relationships between organism and environment, not exotic neuroanatomy, are responsible for unique cognitive capacities. This approach is pertinent to claims about primate cognition; and on this basis, we argue that Vaesen's inference from unique skills to unique mechanisms is unwarranted.

Humans are often observed using multipurpose smartphones to listen to podcasts, surf the Web, and plan international travel. By contrast, even the most sophisticated non-human primates only use single-purpose tools for situation-specific purposes. Whereas wild chimpanzees, for example, use reeds to fish for termites, they never build tools with multiple components and they never use tools in ways that diverge from the situation-specific purpose for which they were created. Put simply, there are undeniable, significant, and manifest differences in the tool-using *behavior* of human and non-human primates. Vaesen maintains that such differences are best explained by reference to evolutionarily discontinuous cognitive mechanisms. He argues that our comparative advantage in eight cognitive capacities suffices to establish "a major cognitive discontinuity between us and our closest relatives" (sect. 1). We disagree.

The term *capacity* has a variety of distinct meanings in the cognitive and biological sciences: It can denote a trait, ability, or mechanism; and although evolutionary pressures sometimes call for the evolution of novel mechanisms, it is generally less expensive to integrate, redeploy, or recalibrate existing mechanisms than it is to build new ones from scratch (Gould & Vrba 1982; Shubin & Marshall 2000; Simon 1996). On the related assumption, that permutations "of the old within complex systems can do wonders" (Gould 1977), even an evolutionary gradualist can acknowledge unique skills while rejecting appeals to new mechanisms. To establish more than the banality that there are uniquely human traits and abilities, Vaesen must demonstrate that these traits and abilities depend on phylogenetically novel wetware. But we hold that his argument is inconclusive, because it ignores a salient explanatory alternative: namely, the hypothesis that cognitively sophisticated tool use depends not on phylogenetically novel wetware, but on the appropriation of social and environmental scaffolding. We invite Vaesen to consider this explanation, for it is simpler than the appeal to unique mechanisms, and therefore preferable even by his own standards.

To make the case for this, we must note that non-human primates use tools in ways suggestive of several (at least) *proto*-human cognitive capacities. Wild chimpanzees and capuchins use tools to obtain food that is out of reach, crack nuts with "hammers," and sponge liquid with leaves (Boesch & Boesch-Achermann 2000; Fragaszy et al. 2004; Whiten et al. 1999); and although neither vervets nor cotton-top tamarins use tools in the wild, both can be trained to do so in the laboratory (Santos et al. 2003). Of course, many non-human primates fail to represent the functional properties of their tools (cf. Povinelli 2000). But wild chimpanzees use different tools at different kinds of termite nests, show selective preferences for different materials, and repeatedly visit nests with reusable tools (Sanz & Morgan 2010) and recent data suggest that they use multi-functional tools (Boesch et al. 2009). Furthermore, captive capuchins can discriminate between functionally appropriate and inappropriate throwing tools (Evans & Westergaard 2006); and looking-time methods reveal that cotton-top tamarins and rhesus macaques perceive changes in functional properties as relevant to tool use, but color change as irrelevant (Santos et al. 2003; for vervets and lemurs, see Hauser & Santos 2007). Finally, repeated experience with tools appears to lead to a more sophisticated understanding of their functionally relevant features (Santos et al. 2003, p. 280).

Next, we contend that an ecologically valid approach to cognition requires attending to both the environment in which traits are expressed and the complex *relationships* between organisms and their embedding environment. Although it is sometimes legitimate and productive to focus on internal mechanisms, cognitive processes (including categorization, inference, and reasoning) are often better understood by reference to coupled organism-environment systems (Hutchins 2008). Consider two uncontroversial examples: When chimpanzees are trained to exploit abstract, symbolic resources, they show a pronounced increase in executive control and inhibition (Boysen & Berntson 1995). Similarly, when human beings supplement their internal capacities for working memory and mathematics with external resources such as pens and paper, we are capable of executing a significantly wider range of computations than we otherwise could (Carruthers 2002; Rumelhart et al.1986). As an organism's capacities are delineated by the tasks it is able to perform, we contend that many capacities are likely to depend on environmental scaffolding (Barrett 2011; Clark 2008).

We suggest that Vaesen should consider the merits of a more ecological approach to uniquely human traits. Relatively minor modifications of primate neuroanatomy (underwritten by the increase in volume of the prefrontal cortex and intimately

coupled changes in evolutionary niches) might have enabled humans to cash in on the informational potential of their environments. Both humans and non-human primates engage in acts of epistemic engineering, construct cognitive niches, and exploit the cognitive potential of their environments (Clark 2006; Sterelny 2003. This dynamic relationship with the environment can increase the sophistication and power of existing cognitive capacities (cf. Beer 2000; Kelso 1995). In many cases, unique capacities are *parsimoniously* explained by reference to coupled organism-environment systems; and where the environment plays the role of cognitive catalyst, we have little reason to appeal to exotic evolutionary mechanisms (Pinker 2010). Finally, such ecological explanations make sense in light of the highly competitive context in which human cognition evolved. Just as corporations often increase their productive capacities by outsourcing production, human brains increase their computational capacity by outsourcing cognitive operations onto the environment. In both cases, we find a marked increase in capacity without expensive changes in internal structure.

We assume that none of these claims will surprise Vaesen, and moreover, that they are not particularly controversial. So perhaps our disagreements are merely terminological. Not only does *capacity* have numerous meanings; so, too, does *unique*. Every species is genetically, behaviorally, and developmentally unique in some respect or other, but Vaesen presumably regards *these* facts as beside the point. At any rate, we hold that terminological clarity and consistency are crucial for discussions of evolutionary uniqueness. Because we are unsure that Vaesen's treatment lives up to this standard, we would like to see a clearer statement of his key terms. For only in light of such a statement could we accurately evaluate the ultimate force of his arguments.

Human tool behavior is species-specific and remains unique

doi:10.1017/S0140525X11001981

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Abstract: Human tool behavior is species-specific. It remains a diagnostic feature of humans, even when comparisons are made with closely related non-human primates. The archaeological record demonstrates both the deep antiquity of human tool behavior and its fundamental role in distinguishing human behavior from that of non-human primates.

In an effort to understand the origins of human tool behavior, investigators have focused on tool behavior in primates, especially in chimpanzees. Nevertheless, tool behavior is widespread and complex in the animal world, as indicated by the survey of Shumaker et al. (2011). This demonstrates that tool behavior evolves through convergent evolution, a point that is most cogently made by examining its presence in capuchin monkeys and birds (Emery & Clayton 2004; Fragaszy et al. 2004), as well as in the great apes. The intense focus on chimpanzees is driven by two factors. First, and most important, is the argument by ancestry: Chimpanzees are the closest living relatives of human beings. The second factor is comparatively trivial, but determines much research: If one studies chimpanzees – and they have received enormous attention for 50 years – any behavior that they demonstrate will be considered intrinsically important.

Vaesen does a remarkable job of assembling the array of evidence separating human tool behavior from the tool behavior of other animals. However, I believe that one line of evidence should have received more emphasis in the paper. In discussing causal reasoning, Vaesen briefly notes the experiments conducted by Povinelli et al. (2000), and presents one example of these experiments (Fig. 1 of the target article). The total corpus of these experiments demonstrates a profound difference in cognition between humans and chimpanzees. The Povinelli monograph underscores the great gulf that exists between human causal reasoning and the reasoning abilities of chimpanzees. In fact, chimpanzees do not seem to have a "theory of how the world works." If this is so, then it epitomizes the unique character of human tool behavior – that it is based on the unconscious, sophisticated knowledge of energy, movement, objects, and the interaction of objects that Povinelli et al. (2000) label "folk physics."

Vaesen elegantly dissects the factors underlying contingent reciprocity in Table 1 of the target article, and is right to point out potential problems with the existence of empathy in non-human primates. Sharing and exchange underlie the division of labor seen in humans, as well as human trade, which is seen indisputably in the archaeological record at about 40,000 years ago. The active teaching discussed by Vaesen is involved in human cultural transmission and the wide dispersal of human culture. Yet, active teaching certainly also underlies human cooperation, and one of the major differences between humans and other animals is that humans habitually cooperate in using and making tools.

In addition to the unique cognitive behaviors underlying human tool use that Vaesen notes, differences in behavior between humans and non-human primates can be documented with stone tools occurring at the earliest archaeological sites, dating to 2.6–2.5 mya. Studies of chimpanzee "archaeology" (e.g., Mercader et al. 2002) only highlight the differences between humans and chimpanzees. Chimpanzees create microscopic stone shatter when they use hammer stones to pound open nuts, but they do not create stone artifacts. In spite of claims that chimpanzees create stone tools that are indistinguishable from the earliest tools in the archaeological record (McGrew 1992), chimpanzee "archaeology" emphatically demonstrates otherwise. Behaviors that frequently are typically associated with the origins of anatomically modern humans actually have a deep antiquity in the archaeological record, going back to at least 1.6–1.4 mya (Cachel 2009). These include greater dispersal ability, spatial organization of behavior at archaeological sites, behavioral variability between sites, transport and curation of stone raw materials and animal carcasses, primary access to animal carcasses whether through hunting or confrontational scavenging, change in stone artifacts through time, and forethought or planning.

Technological selection: A missing link

doi:10.1017/S0140525X11001889

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Abstract: Vaesen's description of uniquely human tool-related cognitive abilities rings true but would be enhanced by an account of how those abilities would have evolved. I suggest that a process of technological selection operated on the cognitive architecture of ancestral hominids because they, unlike other tool-using species, depended on tools for their survival.

Vaesen has produced a convincing descriptive account of the unique cognitive abilities that support human-style tool use. The icing on the cake would be to explain how those abilities may have evolved. What were the selection pressures that made tool-using hominid minds different from the minds of

other tool-using species? Washburn suggested the answer to this question more than 50 years ago:

> Tools changed the whole pattern of life[,] bringing in hunting, cooperation, and the necessity for communication and language. Memory, foresight and originality were favored as never before, and the complex social system made possible by tools could only be realized by domesticated individuals. In a real sense, tools created *Homo sapiens.* (Washburn 1959, p. 31)

A process of *technological selection* would operate when the use of a tool enhances the tool user's fitness. A dependency on tools that conferred fitness advantages may have arisen as hominid ancestors became stranded in increasingly drier open landscapes that offered few places to hide from predators. Even before scrounging for food or having sex, the most important thing those hominids could have done was to protect themselves from being killed and eaten. The solutions they developed to this survival problem would have been under strong selection pressure (Hart & Sussman 2005), and data on modern cases of wild animal attacks on humans indicate that using tools as weapons would have been a very good solution. In a study of 542 animal attacks occurring on all continents, Crabb and Elizaga (2008) found that when victims or passersby used any of 65 different tools to defend against attacking animals, injuries and deaths were significantly lower than when no tools were used. Smart tool use saves human lives in the present, and very likely would have saved the lives of hominid ancestors. One cognitive legacy of this ancestral dependence on tools for protection (albeit not mentioned by Vaesen) may be a preparedness in modern humans to associate aggressive impulses with tools that could be used as weapons (Crabb 2000; 2005; Kenrick & Sheets 1993).

Hominid ancestors who clutched sticks and stones to guard against predators wherever they roamed would have gotten to know their tools quite well. Those individuals with sufficient variants in cognitive abilities would have experimented with and elaborated upon their tools, eventually hitting on the invention of true tools (i.e., tools made by using other tools; Gruber 1969) that would have provided even more survival benefits and additional cognitive and technical challenges.

The differential survival of adept tool users would have contributed to the growth of tool-using culture. A tool-dense culture would in turn influence which genes were subject to selection, and genes that supported the cognitive architecture for sophisticated tool use would be favored (see Laland et al. 2000; Richerson & Boyd 2005). Darwin seemed to have had just this kind of gene-culture coevolutionary process in mind:

> We can see that, in the rudest state of society, the individuals who were the most sagacious, who invented and used the best weapons or traps, and who were best able to defend themselves, would rear the greatest number of offspring. The tribes which included the largest number of men thus endowed would increase in number and supplant other tribes. (Darwin 1871/1981, p. 159)

In this way, the life-saving technological way of life constructed only by human ancestors would have selected the cognitive tunings described by Vaesen.

Unique features of human movement control predicted by the leading joint hypothesis

doi:10.1017/S0140525X11001993

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Abstract: Vaesen suggests that motor control is not among the primary origins of the uniqueness of human tool use. However, recent findings show that cognitive processes involved in control of human limb movements may be much more sophisticated than it was believed previously. The sophistication of movement control may substantially contribute to the uniqueness of humans in tool use.

Vaesen limits the consideration of the motor component of the tool use to two aspects: eye-hand coordination and adaptation of the body schema. However, recent findings show that cognitive processes involved in control of limb movements may be much more complex and diverse. In particular, the *leading joint* hypothesis developed in my lab predicts extensive and sophisticated cognitive processes involved in control of human limb movements. Here I discuss the predicted processes and their relevance to the uniqueness of human tool use.

The leading joint hypothesis suggests that movements are organized by exploiting the multi-joint structure of the limbs (for reviews, see Dounskaia 2005; 2010). The multi-joint limbs consist of chains of approximately rigid segments brought in motion by muscles spanning the joints. During motion, the segments mechanically interact with each other. The leading joint hypothesis suggests that the nervous system benefits from these interactions and exploits them for movement production by introducing a hierarchy among the joints. One (leading) joint is used to generate energy for the entire limb motion, similar to the whip handle that brings in motion the entire whip. Another analogy for the role of the leading joint is towing one vehicle with another. The role of the musculature at the other (subordinate) joints is to modify their passive motion and adjust it to task requirements. An analogy for subordinate joint control is steering the towed vehicle to correct deviations of it from the direction followed by the towing vehicle. Thus, the leading joint generates limb motion and the subordinate joints regulate this motion according to the demands of the task.

The leading joint hypothesis implies that humans use mechanical properties of the limbs to achieve everyday goals in the same way as they use properties of tools. This interpretation suggests that the uniqueness of humans known for tool use may, in part, be observed in limb movements. One can argue that since primates have a similar multi-joint structure of the limbs, the leading joint hypothesis predicts similarity of cognitive processes underlying movement control in humans and primates. This inference may be only partially correct. Indeed, the leading joint hypothesis implies two components of movement planning, each of which may be a source of differences in motor control between humans and primates. The first component is the selection of a leading joint and planning its motion that, after modification at the subordinate joints, can perform the task. The second component is the determination of the subordinate joint control that will adjust the limb movement to the task requirements. Although these two components of movement planning must be present in both humans and primates, the processes involved in human movement control may be more sophisticated.

The superior ability of humans to use leading joint motion for movement production is evident from the vast repertoire of human motor actions. The variety of movements performed during sports activities, dancing, and expressive gestures demonstrates exclusive creativity of humans in exploiting mechanical effects that can be generated within the body through different leading joint motions. This creativity may be a crucial component in mastering diverse tools because each tool changes mechanical properties of the limb in a specific way, and the leading joint motion needs to correspond to these changes.

The subordinate joint control is another possible source of differences in motor performance between humans and primates. Human motor control may be characterized by greater diversity of the ways in which the subordinate joint musculature can modify passive motion caused by the leading joint. This prediction finds support in our recent findings that the modification of passive motion of the subordinate joints requires substantial neural resources. In our experiments, participants performed a

free-stroke drawing task that provided freedom in the selection of movement direction (Dounskaia et al. 2011; Goble et al. 2007). Arm movements were performed through flexion and extension of the shoulder and elbow. Participants demonstrated consistent directional preferences by frequently selecting certain movement directions and strongly avoiding some other directions. The most preferred directions were those in which the subordinate joint moved largely passively. The most avoided directions were those in which the subordinate joint had to rotate in the direction opposite to the passive rotation. Cognitive load created by a secondary task (counting back by 3's from a given number, e.g., "57, 54, 51, . . .," during the performance of the primary, free-stroke drawing task) markedly strengthened the directional preferences (Dounskaia & Goble 2011). These results show that the modification of passive motion at the subordinate joints requires substantial cognitive effort and that humans tend to avoid this effort. It is plausible that this tendency is stronger in primates, who may have limited ability to provide substantial modifications of passive motion at the subordinate joints. However, the capability to accurately modulate passive mechanical effects with muscle activity may be crucial for sophisticated tool use.

To summarize, the interpretation of multi-joint movement control offered by the leading joint hypothesis provides new insights with respect to complexity of cognitive processes involved in motor performance. The idea that the limbs are used as tools for achieving goals of daily life suggests that the uniqueness of humans in tool use may be not limited to the higher levels but presented already at the level of motor control . Obtaining solid support for this hypothesis is a subject for future research.

Brain structures playing a crucial role in the representation of tools in humans and non-human primates

doi:10.1017/S0140525X11001890

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Abstract: The cortical representation of concepts varies according to the information critical for their development. Living categories, being mainly based upon visual information, are bilaterally represented in the rostral parts of the ventral stream of visual processing; whereas tools, being mainly based upon action data, are unilaterally represented in a left-sided fronto-parietal network. The unilateral representation of tools results from involvement in actions of the right side of the body.

In his stimulating target article, Vaesen rightly suggests that the obvious superiority of humans, in comparison with non-human primates, in tool use may result from several (social and non-social) cognitive capacities that differentiate them from other animals. Now, as each of these cognitive capacities is subsumed by specific cortical networks, the problem that I would take into account in my commentary concerns the brain structures that could play a critical role in the conceptual representation of tools in humans versus non-human primates. My commentary will be based on empirical data (obtained in anatomo-clinical studies or neuroimaging experiments, mainly conducted in humans) interpreted according to the principles of the "embodied cognition theories" (Barsalou 2008) and of the "sensory-motor model of semantic knowledge" (Gainotti 2006).

According to these principles, concepts are not represented in the brain in a formal, abstract manner, totally unrelated to the brain processing of sensory-motor functions (e.g., Fodor 1987); instead, they are represented in the same format in which they have been constructed by the sensory-motor system. Furthermore, the brain organization of categorical knowledge reflects the importance of the sensory-motor mechanisms that have mainly contributed to the development of each category.

From the anatomical point of view, these principles predict a close relationship between cortical areas crucially involved in a given category and localization of the sensorimotor mechanisms that have mainly contributed to the development of that category. These predictions have been confirmed by results obtained studying the neuro-anatomical correlates of category-specific semantic disorders and the brain areas activated by different conceptual categories during functional brain imaging experiments (see for reviews Barsalou 2008; Gainotti 2006). Both anatomo-clinical and functional neuroimaging experiments have, indeed, shown that living categories, such as "animals" and "plant life," are bilaterally represented in the rostral and ventral parts of the temporal lobes, because their knowledge is mainly based on the integration of highly processed visual data with other perceptual information. On the contrary, artefacts (and in particular, tools) are unilaterally represented in a left-sided fronto-parietal network, because these categories are mainly based upon action and somatosensory data. Obviously, it is almost impossible to match the brain correlates of the "tools" category in humans and in non-human primates, because, as rightly remarked by Vaesen in his target article, primates in the wild use for food retrieval whatever they come across. Their lack of permanent functional attributions (*functional fixedness*) implies the impossibility of constructing a category characterized by functional features, such as tools. The study of the brain representation of objects in non-human primates has, therefore almost uniquely concerned the ventral stream of visual processing, where important similarities have been found between humans and non-human primates (e.g., Kriegeskorte et al. 2008).

The impossibility of matching the brain correlates of tools in humans and non-human primates does not imply that the analysis of the brain structures playing a crucial role in the representation of tools in humans may not be relevant to understand the brain mechanisms that have allowed the development of the "tools" category and its astonishing complexity in humans. In particular, the left lateralization of fronto-parietal lesions observed in patients with a category-specific disorder for artefacts and the activation of the same left fronto-parietal areas during studies dealing with tools can be explained by two lateralized factors (handedness and language functions) that have been extensively discussed by Vaesen in his target article.

Handedness has been considered as a factor contributing to the development of tools in humans because lateralization enhances manual precision and facilitates motor coordination in social learning tasks. On the other hand, language is deemed to have more contributed to the sophistication of human technologies than to the divergence between humans and other primates in the development of tools. This Vaesen position, which emphasizes more the contribution of handedness than that of language to the tool development is supported by two recent studies, conducted by Lewis et al. (2006) and by Willems et al. (2010) in strong right- and left-handers, to evaluate the role played by asymmetries in motor experience (right-handedness) and by the left dominance for language on the left lateralization of tool representation. In the first study Lewis et al. (2006) have compared the pattern of cortical activation evoked by hand-manipulated tool sounds and by animal vocalizations, showing that tool sounds preferentially evoke activity in high-level motor-related cortical regions of the hemisphere opposite to the dominant hand. In the second study, Willems et al. (2010) used functional magnetic resonance imaging to compare premotor activity associated with understanding action verbs (strictly related to tool use) and showed that right-handers

preferentially activated the left premotor cortex, whereas left-handers preferentially activated right premotor areas. In both studies, therefore, and in agreement with the positions defended by Vaesen in his target article, the laterality of cortical regions activated by the high-level action and tool use was related to right-handedness and not to the left-hemisphere dominance for language.

Human tool-making capacities reflect increased information-processing capacities: Continuity resides in the eyes of the beholder

doi:10.1017/S0140525X11002007

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Abstract: Chimpanzee/human technological differences are vast, reflect multiple interacting behavioral processes, and may result from the increased information-processing and hierarchical mental constructional capacities of the human brain. Therefore, advanced social, technical, and communicative capacities probably evolved together in concert with increasing brain size. Interpretations of these evolutionary and species differences as continuities or discontinuities reflect differing scientific perspectives.

Although once considered a prime hallmark of humanity, tool making has, in recent decades, often been relegated to the ranks of unintelligent behaviors well within the capacity of other animals. Instead, some now postulate that *the* distinguishing feature of humanity is another specific cognitive capacity, such as theory of mind, cooperation, or syntactical language. Vaesen provides an important service to evolutionary scholars by emphasizing two points. (1) Human technological accomplishments far exceed those of chimpanzees. (2) Human excellence reflects a host of advanced, interacting cognitive and motor skills, as opposed to the possession of a single unique cognitive, motor, or social capacity.

Whether human versus ape technological and associated capacities should be labeled "discontinuities" will, however, remain a matter of debate. Behavioral continuities and discontinuities, like beauty, reside in the minds of beholders. Many investigators, for example, routinely interpret animal behaviors within the context of Morgan's Canon. This essentially assures that most animal behaviors will be interpreted as unintelligent – hence, discontinuous with those of humans. Other investigators begin with assumptions that all human cognitive skills derive from animal precursors – and hence, are continuous. Differences also derive from the nature of the observed data. Investigators who primarily study cage-reared animals seem to routinely judge chimpanzees and other apes to be less capable of human-like behaviors than do investigators who study human-reared or wild animals. Similarly, those who study the cognitive and linguistic skills of human infants often seem more open to continuity views than are those who focus on the competencies only of adults or older children. Investigators' views on brain function, however, may be of paramount importance. Assumptions that most unique human behaviors reflect genetically determined, behaviorally specific neural modules predispose to interpretations of discontinuities. In contrast, a focus on developmental neural plasticity and probable brain size–related influences on behavioral functions may predispose to continuity perspectives.

I have previously postulated behavioral continuities between great apes and humans based on three primary considerations (Gibson 1991; 1993; 1996; 2002; Gibson & Jessee 1999): (1) Most traits postulated as uniquely human are eventually found to occur in more rudimentary forms in other animals including great apes: for example, tool making, symbolism, theory of mind, deception, cooperation, culture. In most instances, ape/human differences appear to relate primarily to differences in the amount of information that can be brought to bear on each task and then hierarchically synthesized into new cognitive constructions. (2) Neo-Piagetian perspectives, such as those of the late Robbie Case (1985), postulate quite similar developmental changes across a variety of behavioral domains in maturing human infants and children. Case interpreted these cognitive changes as reflections of developmental increases in information-processing capacities. (3) Irrespective of whatever reorganizational changes may have occurred in the human brain, the most obvious ape/human neuroanatomical differences relate to the overall size of the brain and of many of its component parts (Gibson 1990; 2002; Gibson & Jessee 1999; Gibson et al. 2001) and hence, to probable increases in information-processing capacities throughout much of the brain. The archaeological and paleontological records indicate gradual increases in both brain size and hierarchical capacities, and hence, a probable continuing process of increased information-processing capacities resulting in increasingly advanced cognitive and motor skills. Nonetheless, I view the differences between ape and human behaviors as quite large, much as Vaesen does. Therefore, investigators can have similar views about the distinctions between ape and human capacities, and nonetheless draw different conclusions about continuity or lack thereof. Perhaps, then, they should simply focus on clearly articulating observed animal/human differences and the cognitive and neurological mechanisms perceived to underlie them, rather than on potentially fruitless continuity arguments.

Even if one adopts the information-processing and hierarchical constructional approach, other issues remain. Did hierarchical information-processing capacities evolve first in the tool-using domain and then transfer to other domains (a view Vaesen erroneously attributes to me); did advanced information-processing capacities evolve separately in each behavioral domain; or is hierarchical construction a domain-general process that increased simultaneously in all behavioral domains? Current behavioral and neurological evidence is insufficient to provide a definitive answer to such questions. As Vaesen points out, given that it is the interaction of many advanced human behavioral capacities that distinguishes humans, and in all probability, later fossil hominins from apes, it seems to me most likely that information-processing capacity increased synchronously in many domains.

Vaesen also questions evolutionary relationships between gesture and tool use. Again, he erroneously attributes a hypothesis to me – that manual dexterity first evolved for tool use and then was transferred to the gestural domain. Current evidence seems, if anything, more compatible with the opposite view. In apes, laterality (one component of manual dexterity) is more pronounced in the gestural than in the tool-using domain (Hopkins & Vauclair 2011). At one time, I did adhere to Gordon Hewes's hypothesis that hominin-like gestural communication systems evolved earlier than did hominin-like vocal communication systems (Hewes 1973; Parker& Gibson 1979). This hypothesis, which was based on earlier views that ape gestural capacities exceed their vocal capacities, no longer seems necessary. Recent research indicates that great ape vocal learning capacities are much greater than were previously believed (Slocombe 2011). Moreover, gestural and vocal communications are inextricably linked in modern humans (Goldin-Meadow 2011) and probably were similarly linked throughout human evolution. To the extent that human tool making, communicative, and advanced social behaviors involve similar hierarchical mental constructional capacities and may all have evolved in relationship to the invasion of new foraging niches such as omnivorous extractive foraging (Parker & Gibson 1979), hunting (Vaesen), and/or

scavenging (Bickerton 2009), it seems most likely that advanced communicative (gestural and vocal), social, and tool-making capacities evolved together as one complex whole.

Language and tool making are similar cognitive processes

doi:10.1017/S0140525X11002019

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Abstract: Design features for language and stone toolmaking (not tool use) involve similar if not homologous cognitive processes. Both are arbitrary transformations of internal "intrinsic" symbolization, whereas non-human tool using is mostly an iconic transformation. The major discontinuity between humans and non-humans (chimpanzees) is language. The presence of stone tools made to standardized patterns suggests communicative and social control skills that involved language.

When I wrote "Culture: A Human Domain" (1969), I was attempting to show that the cognitive processes involved in toolmaking (not tool using, as then known in several different animal species) and language were extremely similar, if not identical. If I understand Vaesen's thesis, he has a similar viewpoint (but I would keep toolmaking and tool use as separate processes), and I believe he has extended the analysis well beyond what I attempted and in a most admirable way. I particularly agree with his emphasis on social intelligence and learning, as I earlier suggested that toolmaking was an inherently social process (1967; 1975; 1981; 1996; Holloway et al. 2004), suggesting social consensus and standardization, and thus some element of social control. My emphasis and his differ in that I have always been struck by the arbitrariness of human symbol systems (i.e., language) and by how internal ("intrinsic") symbols become transformed into the external ("extrinsic") symbol systems that can literally define reality – whether it actually exists or not, such as various forms of religious doctrine, not to mention countless historical (and prehistorical) examples of "man's inhumanity to man," such as the Holocaust. These are perhaps "spandrels" of the human dark side and language, and tangential here.

More to the point of language and toolmaking, and to provide a concrete example, I still believe that the transformation of a branch used by chimpanzees for termite fishing is an iconic transformation where the final product is immediately visible in the original product (i.e., stick without leaves visible in a stick with leaves). This contrasts with much of hominid toolmaking – possibly starting with developed Oldowan, and surely present with the Acheulean, Levalloisian, Mousterian, and all blade tools (for in these instances, the final product is an arbitrary transformation where the final product is not necessarily apparent in the prior form but, rather, is a template formed in a social environment). In 1969 I tried to show that the three "design features" (Hockett 1960) considered unique to human language – namely, duality of patterning, productivity, and traditional transmission (the last also present in chimpanzees) – could be assessed in careful analyses of the units making up to the tool making process. For example, the "test-operate-test-exit" (TOTE) paradigm used by Miller et al. (1960) can provide a quantitative as well as qualitative description of making any stone tool, as well as many other activities. Therefore, as crude examples, an Oldowan chopper would be a one TOTE unit tool, if a pebble was hit twice to detach two flakes without rotation. Rotation would add another TOTE unit. An Acheulean hand axe would involve selection of the blank, detachment of flake(s), rotation to other side, detachment of flakes until criteria are met (exit), thus yielding four TOTE units, but with multiple steps in each. Levalloissian flakes would add addition TOTE units. The exact number depends on selection processes for raw materials, as well as the actual flaking and rotating processes. Needless to say, there are also many stone tools where a predetermined shape has been selected because it was very close to the final sought product, as well as properties inherent in stone materials.

After 42 years, I still believe that culture as I defined it then ("that complex whole … shared by man as a member of society … is also the imposition of arbitrary form upon the environment"; Holloway 1969, p. 395) is still an exclusively human domain. The word *imposition* reflects my belief that arbitrary symbol use is not a natural phenomenon and is learned and practiced against psychological and societal resistance. Newer brain imaging, and fMRI studies conducted by Schick and Toth (1993), Toth and Schick (2010), and Stout et al. (2009; 2010), provide some tantalizing co-occurrences between complex motor patterns for stone tool knapping and the motor areas for language in Broca's region as well as the occipital and parietal lobes.

Nevertheless, as our understanding of non-human animal behavior is enhanced with both field and laboratory studies, it is likely that only language will remain the essential divide between us and other animals.

Not by thoughts alone: How language supersizes the cognitive toolkit

doi:10.1017/S0140525X11002020

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Abstract: We propose that Vaesen's target article (a) underestimates the role of language in humans' cognitive toolkit and thereby (b) overestimates the proposed cognitive discontinuity between chimps and humans. We provide examples of labeling, numerical computation, executive control, and the relation between language and body, concluding that language plays a crucial role in "supersizing humans' cognitive toolkit."

In the target article, Vaesen notes a remarkable discontinuity between humans and chimps in tool use and cognitive features. Language is suggested to play a merely facilitative role for other cognitive functions. We propose that Vaesen (a) underestimates the role of language in humans' cognitive toolkit and thereby (b) overestimates the proposed cognitive discontinuity between chimps and humans.

Language can be considered, in Clark's words (2008), as a mind-transforming cognitive scaffold. It can productively transform people's cognitive capacities by simplifying their outer world. For instance, the simple act of labeling creates a new constellation of "perceptible objects" and reconfigures the problem space (Clark 1998a), thereby increasing people's computational ability enormously. Consider numerical computation as another example. Dehaene and colleagues (1999) proposed that when people use number words to complement more basic biological capacities, people acquire an evolutionary novel ability to deal and think about *unlimited exact* quantities, hinging crucially on language. Systematic skill improvement attempts, fault detection, and corrections of flaws in people's own planning – to mention only few – are the result of the interaction of biological brains with linguaform resources that together allow "thinking about thinking" (Bermudez 2003; Clark 1998b; 2008). As such, language opens up new computational opportunities, enabling

humans to solve complex problems. This may be the case for some (if not most) of the cognitive tools that Vaesen points out in his target article.

Furthermore, we agree that one cannot easily determine the evolution of language (cf. Richerson & Boyd 2005). Yet, it is undisputed, also by Vaesen, that language has been particularly useful for participating in culture, in particular in keeping track of complex relational systems (i.e., gossip). However, relatively simple forms of communication are not unique to humans; the most primary vocalizations even seem to be present in primates, which often participate in relatively simple relational systems (Dunbar 1997). As such, language seems to have developed *primarily* for purposes directly related to social interactions, becoming more important once people began living in larger groups. Language has since become immensely important for other cognitive tools. Clark even suggested that the "recent intellectual explosion in evolutionary time is due as much to linguistic-enabled extensions of cognition as to any independent development in our inner cognitive recourses" (Clark 2008, p. 232).

This point is further exemplified by recent work in (social) psychology. As an example of two of the cognitive tools Vaesen put forth – executive functioning and body plasticity – we know that both chimps and humans show relatively simple and automatic affiliative behaviors in response to an angered interaction partner (Häfner & IJzerman 2011; Preuschoft & Van Hooff 1997). Humans, however, seem to have the unique capacity to control the self to accommodate for the other in committed relationships (Rusbult et al. 1991). One could wonder to what extent similar behaviors may occur in other species that display monogamous pair bonding.

Yet, the simple fact that humans possess advanced abilities to postpone immediate self-interest (i.e., self control) in relation to negative emotions like anger (and their facial expressions) is not surprising, as language has been shown to closely rely on modality specific representations that guide and help people's cognition (e.g., Pulvermüller 2005; Zwaan & Taylor 2006). Verbs (indicative of action; compared with adjectives) related to smiling or frowning induce greater activation of zygomaticus or corrugator muscles (Foroni & Semin 2009). In addition, physically warm (as compared with cold) conditions induce people to use more relational language (verbs; IJzerman & Semin 2009). One might logically propose that linguistic features play a vital part in actions and thoughts above and beyond "merely" "extending the body." Research suggests it can. Linguistic features permit to represent close and near "future" at different abstraction levels, allowing people to coordinate and plan future joint and individual actions (Clark & Semin 2007).

In short, whether it is for computational purposes or for social interaction, language allows complex uses for otherwise simple elements and thoughts. Language not only allows new uses of people's outer worlds, but it also allows an "intellectual explosion" because of an exponential increase of the utility and potential of existing tools. Taken together, we think that the "discontinuity" between humans' and chimps' tool use may be misleading. Indeed, our suggestion seems to find support in work on conceptual knowledge; research shows that both for human and nonhuman animals, the presence of a specific object (e.g., a conspecific or food) activates knowledge distributed across modality-specific systems, rather than through modular and amodal systems (see Barsalou 2005).

We have proposed that differences between humans and chimps in tool use are not due to a discontinuity between humans and chimps, but, instead, due to a vast discrepancy enabled by the language that provides immensely complex usages of otherwise relatively simple cognitive tools. Language thus complements otherwise basic biological abilities, thereby providing a key factor in the differentiation between humans and chimps.

For these reasons, language plays a fundamental role not only in the development of tool use, but also, and most importantly, in creating culture accumulation. Vaesen's discussion on cumulative culture surprisingly omits the important and, we argue, *necessary* role of language in building complex systems and in the development of human technology.

Can object affordances impact on human social learning of tool use?

doi:10.1017/S0140525X11002032

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Abstract: The author describes "higher" and "uniquely human" sociocognitive skills that he argues as being necessary for tool use. We propose that those skills could be based on simpler detection systems humans could share with other animal tool users. More specifically, we discuss the impact of object affordances on the understanding and the social learning of tool use.

Vaesen speculates that the human capacity to learn novel tool use from observing goal-directed movements performed by others (Csibra & Gergely 2007) is a hallmark of our uniqueness, and that it is based on "higher" sociocognitive skills. It has been proposed that such skills were supported by the ability to (1) decode kinematic information into causal relationships between a behavioural sequence and its result (Gergely 2007); (2) interpret others' behaviors as rational (assuming that the most efficient observed action means are adopted to achieve a particular goal; Gergely & Csibra 2003); and (3) accumulate *a priori* knowledge from past observations about agents' intentions and behaviours in order to predict future events (Chambon et al. 2011).

We agree with the author that the sophistication of such sociocognitive skills goes far beyond those of any other animals'. Yet, we believe that this sophistication could also be the result of simpler systems allocated to the detection of low-level, local sources of information, such as the manipulative properties of objects called "affordances."

Affordances define relational properties that emerge from matching the perceived physical features of objects and the agent's biomechanical architecture, goals, plans, values, beliefs, and past experiences. We propose that affordances allow agents to delineate the number of candidate motor acts that could be performed on tools. We postulate that affordances constrain the number of possible solutions by generating biomechanical prior expectations in line with the bodily architecture of agents. These priors would bias individuals to act towards objects aiming at biomechanical optimization (Rosenbaum et al. 1996; Weiss et al. 2007).

As the author rightly points out, compared with other animals', the many degrees of freedom characterizing human effectors and their striking motor control considerably enhance our ability to detect new affordances and new potential objects uses. All this contributes to increase the variety of the behavioural repertoire. Nonetheless, we are sceptical about the idea that the primary advantage such architectural properties bring for tool use acquisition is fine-grained social learning. Indeed, in many situations, detecting tools affordances allows learners to avoid such a

high-level but costly strategy. Instead, this biomechanical uniqueness could increase the probability of individual innovation, particularly in situations where novel tools are physically unstructured and multi-purpose. For example, Acheulean stone tools are poorly structured and roughly symmetrical objects with a cutting edge. They do not offer affordances salient enough to constrain the number of candidate motor acts that could be performed on them. Sterelny (2003b) points out that the exact functions and uses of Acheulean stone tools, although they were the dominant element of human technology for more than a million years, remain a matter of debate. It is more plausible that our ancestors – who were predisposed to behavioural innovation thanks to their high biomechanical flexibility – progressively discovered not one or two, but a multitude of tasks that Acheulean stone tools could roughly carry out.

We argue that the evolution of the human technological environment favoured the utility of simpler systems such as affordances detection. This eases the negotiation of the highly demanding cognitive problems of tool use learning (Clark 1997; Dennett 1995; Sterelny 2003a; 2003b). Indeed, tools we interact with daily are designed for specific purposes. Affordances that are available through their complex physical attributes offer the chance for naive users to extract their functions at low cost (Dennett 1982; 1995; Gregory 1981; Norman 1988). In our engineered environments, affordances play a crucial role in the acquisition of tool skills through individual trial and error as well as social learning. More specifically, we argue that perceiving affordances directly biases the understanding of tool behaviours performed by others, and consequently the extraction of related functional knowledge. The biomechanical priors that emerge from the perception of tools affordances constrain the number of candidate motor acts an individual could initiate. Similarly, they also tune the observer's prior expectations about which motor behaviors are most likely to be performed by others, enhancing the predictability and learnability of novel tool use. Learning about a novel tool from observing a demonstrator using it in a biomechanically "rational" way would be less costly than learning from a demonstrator that violates our expectations. That is, the convergence of the demonstrator's and observer's biomechanical expectations facilitates an efficient learning strategy, based on kinematics, rationality principle, or prior knowledge.

Taken together, these observations question the exact role of high-level, fine-grained social learning in the acquisition of new tool skills. Relevant to this is work addressing animal behavioural "traditions" – behavioural patterns that are relatively stable in groups and are at least partly maintained by some forms of social learning. These could result from constraints that limit the number of possible alternative behaviours, more than from the robustness of high-level social transmission mechanisms (Claidière & Sperber 2010; Tennie et al. 2008). Here, we posit that the crucial role affordances play in the acquisition of tool use strongly suggests that fine-grained social learning strategies, such as true imitation of observed action goals and means, are sometimes less important than previously assumed. In fact, affordances, together with ecological constraints and other products of epistemic engineering, could enhance the effectiveness of more frugal forms of socially directed learning (Acerbi et al. 2011; Franz & Matthews 2010) such as emulation learning (i.e., the observer copies action goals performed by a demonstrator without considering action means) or even stimulus enhancement (i.e., when an individual directs its behaviour towards an object or a part of an object with which it saw another individual interact).

ACKNOWLEDGMENTS

This work was supported by the FP7 project ROSSI, Emergence of communication in RObots through Sensorimotor and Social Interaction, European Commission grant agreement no. 216125.

We are grateful to Janet Bultitude, Karen T. Reilly, and Alberto Acerbi for their helpful comments on earlier versions of this commentary.

Thinking tools: Acquired skills, cultural niche construction, and thinking with things

doi:10.1017/S0140525X11002044

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Abstract: The investigative strategy that Vaesen uses presumes that cognitive skills are to some extent hardwired; developmentally plastic traits would not provide the relevant comparative information. But recent views of cognition that stress external resources, and evolutionary accounts such as cultural niche construction, urge us to think carefully about the role of technology in shaping cognition.

Vaesen should be congratulated for proposing a multifaceted account of a human uniqueness. Too often, hypotheses of human uniqueness posit a single breakthrough, with a subsequent cascade of other traits. Vaesen, to his credit, offers a package of cognitive skills that he believes underlies a single unique trait: cumulative cultural evolution. However, the comparative method that Vaesen uses to get to this package of cognitive skills is problematic. By engaging in straight comparison of chimp and human cognitive skills, Vaesen omits the possibility for the co-evolution of cognition, technology, and culture that potentially underpins human uniqueness. The comparison also presumes that these traits are not developmentally plastic.

The co-evolutionary picture is important given recent models of cognition that emphasise the importance of the external world in cognitive processes and the acquisition of cognitive skills (Clark 2008; Clark & Chalmers 1998; Menary 2010; Sterelny 2010a) and neural plasticity (Quartz & Sejnowski 1997). In particular, the hypothesis of cultural niche construction of Kim Sterelny argues that these human interactions with the world are important for human cognitive evolution. The developmental and cultural environment of hominins helps shape cognitive processes (Sterelny 2003; 2010b; 2012). Tools, and the behaviours of other tool users and makers, can act as scaffolds to cognition.

Moreover, Vaesen never mentions how his list of cognitive skills gets "in the head" of humans; but the assumption that drives the comparative method is that the skills are evolved and hardwired traits. Co-evolutionary models such as niche construction offer an alternative developmental route for these skills.

We can see the potential impact of these alternative models of cognition in relation to the Acheulean tool culture that Vaesen briefly discusses in the second part of his article. Vaesen suggests that there is not much variability in Acheulean tool form, and that it lacks evidence of cumulative development. Consequently, Vaesen infers that the associated cognitive skills he thinks are necessary to possess a cumulative culture are therefore absent.

However, many archaeologists point out that there is in fact a great deal of variation in tool manufacturing methods, materials, and raw material resource strategies (Lycett & Cramon-Taubadel 2008; Lycett & Gowlett 2008; McNabb et al. 2004; Sharon 2009). So whilst tool form, and possibly even tool use, is fairly constant, tool manufacturing methods do in fact show some signs of cumulative culture. So, the evidence for Vaesen's package of cognitive skills *is* potentially present in manufacturing methods, even if it is absent from the final tool form. Lycett and Gowlett (2008) suggest that this is the result of transmission between generations that allows for the accumulation of variation in manufacturing skills but fails to transmit and accumulate variations in tool form. Using ideas about the co-evolution of culture and cognition, and acknowledging the role that external resources play in cognitive processes, we can make sense of this contradiction.

As a social animal, hominins may take the presence of tools and other toolmakers as physical and behavioural templates for their further tool production. Hominins or modern sapiens making a

tool can use as a template other tools possessed by individuals in their community. Consequently, the "idea" of a tool need not be "in the head" of an individual, as tools possessed by other members of the group can play this role. There are any number of external resources that can assist individuals to stay "on track" in their manufacturing task.

This social world is crucial in learning to make tools. Other toolmakers are accessible behavioural templates of toolmaking activities. Tools, and other tool users, create an environment that can support the development of cognitive skills associated with tool manufacture. Tools are made in a world where there are other people making tools, and where there is close contact between toolmakers and their behavioural outputs. For a young hominin learning to make a tool, this environment provides a situation where the cost of learning a tool is relatively low. There are lots of behavioural templates around, some of whom may even have a genetic interest in ensuring the young hominin acquires the appropriate skills (Sterelny 2010b; 2012).

In his section on executive control (sect. 12.2), Vaesen notes that individuals with certain brain lesions can achieve complex sequences of tasks where there is clear "next steps" available in the form of environmental cues (the lunch box packing case; sect. 6) but cannot achieve tasks where purely mental planning is necessary (Tower of London tasks; sect. 6). For a social organism, tool manufacturing quite likely resembles the first task, with abundant physical props and a community of users and makers. Tools may scaffold executive control (Jeffares 2010b).

Therefore, we can resolve the apparent paradox of the Acheulean by understanding the environment that the tools are made in. Acheulean tools are made in a social context; and being members of a toolmaking community buffers the transmission of skills, reduces learning costs, and allows variation to develop. Nevertheless, the hominins that made these tools appear to not have the capacity to accumulate technological improvements in tool form. This suggests that suitable buffering effects were not present during deployment activities, or that different processes encouraged standardisation of tool form (Jeffares 2010a).

Regardless of the details of this case, what should be clear is that we have to acknowledge that cognitive skills do not straightforwardly facilitate technological accumulation. There is a cognitive ecology of co-evolutionary processes, external resources, scaffolds, and developmental influences that shape human cognition, both now and in the past. This matters to understanding human uniqueness and how it evolved.

Humans make tools because they live in a unique cultural environment that helps them learn, and fine-tune, the cognitive skills necessary for toolmaking. To understand cumulative culture, we must understand how culture scaffolds the learning of cognitive skills, and not presume the skills that underlie it. By not considering the historical environment and the external environment as part of that matrix of forces that shapes cognition, Vaesen potentially ignores the possibility that some of his package of cognitive skills are learnt.

Tool use induces complex and flexible plasticity of human body representations

doi:10.1017/S0140525X11001907

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Abstract: Plasticity of body representation fundamentally underpins human tool use. Recent studies have demonstrated remarkably complex plasticity of body representation in humans, showing that such plasticity (1) occurs flexibly across multiple time scales and (2) involves multiple body representations responding differently to tool use. Such findings reveal remarkable sophistication of body plasticity in humans, suggesting that Vaesen may overestimate the similarity of such mechanisms in humans and non-human primates.

Vaesen presents a compelling and comprehensive overview of the cognitive abilities underpinning human tool use. Across diverse domains, Vaesen argues for important differences between humans and other primates in all but one. Here we focus on this last domain, body schema plasticity, which Vaesen suggests may not differ substantially between humans and apes. Although we agree that the fact of body schema plasticity characterises both human and non-human primate cognition, recent results have revealed a highly complex relation between plasticity of body representations and tool use in humans. We suggest that there are likely to be fundamental differences in such mechanisms between humans and other primates, with important implications for tool use and its relation to other cognitive abilities. In particular, we focus on two main issues: (1) the time course of plasticity in humans occurs flexibly across multiple time scales, and (2) multiple body representations coexist in the human brain, responding with differential plasticity in the context of tool use, and accounting for the different kinds of experience associated with different types of tools.

Apes and monkeys in the wild rarely use tools spontaneously, and they learn to do so only after long and laborious training (Iriki & Sakura 2008). In humans, however, tool use induces plasticity at multiple time scales, showing long-term learning in the case of specific expertise, but also flexibly changing over just a few seconds in experimental situations. For example, some studies have varied tool use on a trial-to-trial basis, finding clear modulation of peripersonal space representations depending on whether or not a tool is used (Holmes et al. 2007) or what length tool is used (Longo & Lourenco 2006), demonstrating that tool use induces nearly instantaneous plasticity. Other recent studies have demonstrated long-term plastic changes associated with expertise for specific tools. In blind cane users, for example, merely passively holding the cane extended auditory-tactile interactions along the length of the tool; in control participants, by contrast, active training with the cane was required to induce such extension (Serino et al. 2007). Analogous findings have been reported for everyday use of the computer mouse (Bassolino et al. 2010): Merely holding a mouse in the hand habitually used to control the mouse (the right) extended auditory-interactions to the space near the screen; whereas such effects were found only when the mouse was actively used, and not just passively held, in the hand *not* habitually used to control the mouse (the left). These results demonstrate that tool-induced plasticity is highly complex, occurring across multiple time scales and levels of abstraction.

Although the human brain certainly treats wielded tools at some level as if they were extensions of the body, distinctions between the body and tools must also be made, and at several levels. For example, Povinelli et al. (2010) rightly point out that one important function of tools is to allow actions that would otherwise be prohibitively dangerous, such as reaching into a fire or stirring a pot of boiling soup. In such cases, effective guidance of the tool may require it being treated as part of the body, even as safety considerations may necessitate it being strongly distinguished from the body. Such conflicting requirements highlight the need for multiple body representations, maintaining parallel, and potentially inconsistent, representations of the body with or without the tool.

This flexibility appears much less pronounced in non-humans primates: In monkeys, long-term tool use trainings induce structural changes in neural body representations, which are rigid and persist whether the animal is tested with the tool or without

(Quallo et al. 2009). In humans, conversely, long-term tool use expertise develops multiple body representations, which can be selectively activated depending on the presence/absence of the tool. In blind cane users, for example, peripersonal space representations were extended towards the far space, or limited around the hand (as in sighted subjects), depending on whether blind subjects held their cane during testing (Serino et al. 2007).

It is also interesting to note that in humans, the subjective experience of wielding a tool is strikingly different from that of illusions, such as the rubber hand illusion (Botvinick & Cohen 1998), in which external physical objects are treated as being part of the body. This dissociation suggests that the tool is "embodied" at a lower, more implicit level, what De Preester and Tsakiris (2009) refer to as "body-extension," distinguishing it from the higher-level, more conscious "body-incorporation" seen in the rubber hand and related illusions. An interesting, intermediate case is that of prosthesis implantation: A prosthesis is a tool, extending action potentialities of an accidentally limited body; but prostheses also replace the shape of the missing limb, hence restructuring the physical body. There seems to be wide variability in amputees' experiences of their prostheses, from those who experience the prosthesis as a corporeal structure to those who consider it an artificial device (Murray 2004). It is probable that both functional (level of motor control) and cosmetic (level of anthropomorphism) features of the prosthesis underlie such differences. Recent findings suggest that the sense of ownership over a prosthesis can be enhanced by illusory (Ehrsson et al. 2008) or physical (Marasco et al. 2011) sensory feedback to the stump. This level of abstraction in the experience of body incorporation of artificial objects cannot be investigated in non-human primates (Graziano 1999).

We suggest that different levels of body schema plasticity characterize human cognition and might account for the different experiences associated with the multiplicity of complex tools used by humans in everyday life. These and other recent findings have provided fundamental insight into the role of plasticity of body representations in human tool use. Together, they suggest that body schema plasticity is a highly complex, flexible, and task-dependent process, which should not be thought of as simple "present or absent" in an organism or species. Therefore, we believe Vaesen has too quickly excluded an important role for this factor as an important source of differences between human tool use and that of other primates.

Prosthetic gestures: How the tool shapes the mind

doi:10.1017/S0140525X11001919

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Abstract: I agree with Vaesen that it is a mistake to discard tool use as a hallmark of human cognition. I contend, nonetheless, that tools are not simply external markers of a distinctive human mental architecture. Rather, they actively and meaningfully participate in the process by which hominin brains and bodies make up their sapient minds.

> If we could rid ourselves of all pride, if, to define our species, we kept strictly to what the historic and the prehistoric periods show us to be the constant characteristic of man and of intelligence, we should say not *Homo sapiens*, but *Homo faber*.
>
> — Henri-Louis Bergson, *Creative Evolution* (1911/1998, p. 139)

Despite the famous feats of termite-fishing chimpanzees and hook-crafting crows, Bergson's words from his *Creative Evolution* remain largely unchallenged (for a good review of the evidence, see Seed & Byrne 2010; Tomasello & Herrmann 2010). Even the most highly trained nut crackers could not manage to equal the abilities seen in the earliest hominin stone tool makers (Davidson & McGrew 2005; Iriki & Sakura 2008). There is more to the notion of *Homo faber*, however. For it is not the sheer variety and sophistication of human technologies, but rather the profound complexity of our engagement with tools and technologies that matters the most: We humans alone define and shape ourselves by the tools we make and use. Inspired from the work of Bernard Stiegler (1998) and André Leroi-Gourhan (1963/1993), I would like to describe human tool use as the *prosthetic gesture par excellence* (Malafouris 2010a). This is a species-unique and self-transforming human predisposition that leaves very little space for valid relational comparisons with other animals (or so I wish to suggest).

I understand that those committed to the long-held evolutionary ideal of a cognitive "continuum" between human and nonhuman animals would probably take my previous points as ill-conceived and anti-Darwinian: "The difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind" (Darwin 1871, p. 105). But I think that so far as the human entanglement with tools is concerned, Darwin's claim is rather misleading. What must have certainly started as a difference in *degree* soon became one of *kind* – that is, a difference that makes a difference. No doubt, the lack of conceptual clarity about the use and meaning of terms such as *degree, kind, mind*, and *tool* is a major contributing factor for our troubles with the question of "human cognitive autapomorphies" (Suddendorf 2008, p. 147), and I am afraid Vaesen's paper does very little to help us clear the ground.

In any case, the interesting question is not whether human and animal tool-using abilities are different, but rather, why they are, and how did they become so different. Where do we start, then? Mainstream approaches to the comparative study of cognition follow two main paths when it comes to answering those questions: The first seeks to explain apparent discontinuities in human mental function as the natural outcome of the human genome, that is, resulting directly from biological adaptations (e.g., the "supermodule" hypothesized by the relational reinterpretation [RR] hypothesis proposed in this journal by Penn et al. 2008). The second path seeks to account for the differences between human and nonhuman cognitive abilities by way of language, culture, learning, and the external symbolic representational means that these capacities afford (e.g., Tomasello et al. 2005; Tomasello & Herrmann 2010). The former path takes us into the realm of biology; the latter into the realm of culture.

Vaesen's approach combines both paths. His thesis is essentially that humans are born with better-equipped neural systems and cognitive machinery, which is sufficient to account for the discontinuity between human and nonhuman animal tool use capacity even in the absence of culture. He then shows how our superiority with respect to the nine cognitive capacities deemed crucial to tool use can also explain why technological accumulation evolved so markedly in humans. In other words, the aim of his study is not to question the barrier between "individual brain power" and "culture," (sect. 1) but instead to argue that human superiority is reflected at the former biological level as much as it is in the latter sociocultural level: "[h]uman tool use reflects higher social intelligence (indeed), but just as much greater non-social wit" (sect.1, para.2).

Here is, then, the nub of the problem – at least as I see it: Whilst Vaesen's comparative gaze seems squeezed *within* the artificial boundaries that separate the cultural from the biological realm, the sort of things we call tools stubbornly inhabit the hybrid realm *between* – that is, the realm where brain, body, and culture conflate, mutually catalyzing and constituting one another (Malafouris 2008; 2010b). As a result,

Vaesen's account leaves out some of the issues that I believe matter the most. For example, the human total reliance on tools (Schiffer & Miller 1999) and their role in what Andy Clark calls "supersizing the mind" (2008), or the possibility that the cognitive *discontinuity* between us and our closest relatives may be largely the product of the cognitive *continuity* of human brains, bodies, and tools.

Is there any way out of this? I believe that searching for the neural and cognitive bases of tool use provides useful pointers but cannot in itself explain the unique ways humans and tools bring each other into being – especially when grounded in a strictly "internalist" and "computationalist" view of mind, as is the case of Vaesen's paper. The question of human tool use is not one that can be answered by looking deeper into the human brain; it demands a holistic anthropological stance (in both the philosophical and the cognitive sense). We need to start thinking about human tool use as a transformative constitutive intertwining of neural, bodily, and material recourses, rather than in terms of a pre-specified set of adapted neural structures and cognitive functions (see Malafouris 2010a; 2010b; Wheeler & Clark 2008, p. 3563). This approach to the study of human tool use could also help us to avoid the long-exposed but still engrained anthropocentric prejudices that any discussion of non-human animal tool use inevitably embodies (Hansell & Ruxton 2008). Moreover, it will lead us to ask questions not simply about how the mind shapes the tool, but also about how the tool shapes the mind.

Cathedrals, symphony orchestras, and iPhones: The cultural basis of modern technology

doi:10.1017/S0140525X11001920

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Abstract: The distinctions drawn by Vaesen are plausible when we are comparing chimpanzees and human beings somewhere between the middle Paleolithic and the Neolithic. But since then new kinds of organization have vastly outstripped these neurological differences to account for the enormous advancement of human technology – from cuneiform to the iPhone – leaving our remarkable evolutionary cousins far behind.

> *Never let overwhelming similarities obscure fundamental differences.*
>
> — Leslie A. White, personal communication (ca. 1960)

I think that Vaesen's article is exemplary in characterizing the differences between human and ape technology until about the beginnings of the Neolithic. Since then ape technology seems unchanged (except for a few items some captive apes may have learned from humans). Note that my argument is not meant to diminish apes; they are, on their own terms, utterly amazing creatures. Chimpanzees can, for example, do dentistry (McGrew & Tutin 1972) (Fig. 1).

And I will always be in awe of Gombe's Figans, who, at just the right moment, quietly announced impending danger, scattering the whole troop and leaving the newly opened box of bananas all to himself (Rappaport 1979). Such creativity and imagination with such modest tools are remarkable.

It seems plausible that some neurological capacities account for the differences between apes and pre-Neolithic humans; but since then, the explosion of technology, science, knowledge, and religion is due not to anything particularly neurological but to things explicitly cultural. Things like:

Figure 1 (Moerman). Belle is removing Bandit's loose tooth with a small stick while Shadow observes. Copyright © W.C. McGrew.

Village life – with technological specialization, emerging immediately after the first plant and animal domestication, requiring defensive fortifications to protect stored food and seed against raiders, implausible for individuals, but relatively simple for a group with some leadership (utterly novel 10,000 years ago).

Transportation – allowing the easy movement of people and things over vast distances starting with, say, the Silk Road; then the development of shipping (sails, compasses, accurate clocks); then trains, cars, and trucks; then 2,000 contemporary airlines moving 2 billion passengers per year (increasing at about 5% a year, hence, doubling in 15 years).

The sharing of knowledge – ranging from things such as the Rosetta stone, both the actual one and the language-learning computer program; the Google project to scan and make available all the books ever written; the huge explosion of education, and particularly higher education, making the most sophisticated thought and practice available retail (currently, more than 80,000 Chinese students are enrolled in colleges and universities in the United States; 37% of students at the University of Michigan are from abroad).

Cell phones – a while ago I read that half the people in the world had never made a phone call; but today, about 60 people per hundred own cell phones, and many of those who don't will live in homes with people who do; the first mobile phone (a car phone) appeared in the mid 1950s; countries with relatively few cell phones are political dictatorships, where leadership prohibits them (Burma, Laos, Cambodia).

Symphony orchestras.

The instantaneous emergence of whole new global technologies – for example, the iPhone was first sold mid-year 2007; by the beginning of 2011, more than 300,000 "apps" were available for the iPhone; as I write this 7 months later, there are an additional 125,000, that's 18,000 new ones per month; the iPhone 4S5 with Siri, the personal assistant, is just out.

Computer fluency – There are about 11 million people in the world fluent in one or another computer programming language; more than 3 million[1] (others estimate 4 million) of them use C++, arguably more than any other computer language.

None of these things, or things like them, are due to changes in the brain. They are due to innovations in the way people can work collectively at vast projects such as building a medieval cathedral (probably the first truly international industry)[2] or the World Trade Center in Bahrain.[3] They are due to the fact that thousands of otherwise ordinary individuals are acting in coordinated ways to achieve otherwise impossible outcomes; lately not so much in gangs but in networks. Imagine how many people have a hand in manufacturing a Toyota.

None of this hinges on brain changes. These things hinge on how our brains are used (or maybe how they use us).

The medieval cathedrals are an excellent case in point. They were constructed with only the very simplest machines: wedges, pulleys, levers. Many of the techniques used, particularly in the forming of vaults, are unknown to us; some restorers of 600-year-old cathedrals (e.g., E. E. Viollet le Duc, who rebuilt Notre Dame between 1845 and 1864) have made many ingenious inferences and have helped us to understand what seems almost impossible (Reiff 1971). Some of these magnificent buildings were under construction for 200 years. And most of them were, in effect, built of wood by carpenters; masons then laid stone over the wood, the wood then removed, leaving what we see today. Wrote Viollet le Duc in about 1860:

> A well-made scaffolding is a feature of the builder's art which engages his best intelligence and his thorough supervision, for the real skill of the builder can be judged from the manner in which he places his scaffolding.... If the scaffoldings are massive, if they employ wood in profusion, the [subsequent] workmen are well aware of it: they judge the chief's degree of practical knowledge from this provisional work, and they recognize any inclinations of his from his abuse of means.... [T]he very lives of his workmen depend on it. (Fitchen 1961)

Here we see the art of scaffolding: intelligence, supervision, teamwork, skill, awareness, life itself – that is, leadership. And when done, it is torn down.

This is all organization, cooperation, planning, teaching, engaging the skills of hundreds or thousands of different people with different background and training to make a cathedral or an iPhone. Without offense, we see nothing like this in chimpanzees.

NOTES

1. This estimate is a personal communication from Dr. Bjarne Stoustrup, the designer and implementer of the C++ programming language.

2. Google "Reims cathedral images" for a spectacular example, one of hundreds.

3. Google "Bahrain Trade Center images."

Childhood and advances in human tool use

doi:10.1017/S0140525X11001932

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Abstract: Human life history incorporates childhood, a lengthy post-weaning period of dependency. This species-specific period provides an opportunity for extensive learning and for sophisticated cultural behaviors to develop, including crucial tool use skills. Although I agree that no individual cognitive trait singularly differentiates humans from other animals, I suggest here that without childhood, the traits that are key to human tool use would not emerge.

When Jane Goodall (1998) first reported that chimpanzees strip leaves from twigs to fish for termites, Louis Leakey famously responded: "Now we must redefine tool, redefine Man, or accept chimpanzees as humans." The decades of research following Goodall's discovery have convincingly rendered invalid any description of *Homo sapiens* that places us as the planet's only tool-making animal. Yet we remain without peer when one considers the depth, breadth, and inventiveness of our tool use. Vaesen's claim that the way we use tools constitutes a major cognitive discontinuity between our closest relatives and ourselves is staked on solid ground. Standing out in his coverage of tool-related cognitive traits is a reliance on experimental comparisons of human children and adult chimpanzees. In this a critical point is missed: Ours is the only species to have a childhood as a life stage, something that likely lies at the heart of the discontinuities Vaesen outlines.

The majority of mammals follow birth with a period of infancy (characterised by the appearance of deciduous teeth and all or some nourishment being provided by maternal lactation) that transitions seamlessly into adulthood. Chimpanzees postpone puberty and insert an extended phase of juvenile growth between infancy and adulthood whereby offspring are dependent on their mothers for about 5 years (Kaplan et al. 2000).

Humans have a shorter infancy and, at least in preindustrial societies, breast-feeding is usually discontinued around the beginning of the third year (Kaplan et al. 2000; Sellen & Smay 2001). Weaning at this young age places a great nutritional burden on offspring. Three-year-olds are not typically mature enough to prepare their own food and are too limited by deciduous dentition and a small gastrointestinal tract to consume an adult diet. In various hunter-gatherer societies, the solution to this problem is for older members of the social group to provide specially prepared foods that are high in energy and nutrients until self-care becomes possible at around 7 years (Locke & Bogin 2006). This post-weaning pre-juvenile stage constitutes "childhood" and corresponds with a distinct, species-specific growth curve and changes in sex-hormone patterns (Bogin 1990; Hochberg & Albertsson-Wikland 2008).

The insertion of childhood as a life stage not only lengthens the period of dependency on others, but also places responsibility of care for the child with the community. By contrast, chimpanzees transition directly from infant dependence on the mother to independent juvenility. Human childhood therefore affords an extended period of development during which offspring are provided multiple opportunities for learning from the broader community while buffered from survival pressures incumbent on juveniles and adults. These opportunities will be enhanced by the uniquely human practice of teaching. The slow somatic growth and delayed sexual maturation of childhood serve to maximize maturational differences between adult teachers and child students, differences that allow a great deal of learning, practice, and modification of survival skills (Bogin 1990).

Associated with adult-child instruction is the tendency of children to replicate all of the actions an adult uses when achieving an object-directed outcome, even actions whose relevance is shown to be causally redundant (see Nielsen & Blank 2011). This "over-imitation" facilitates the rapid acquisition of skills, actions, and behaviors while avoiding the potential pitfalls and false end points that can come from trial-and-error learning. Indeed, children are not particularly good at innovating even simple tools (Beck et al. 2011). Though traces can be found in the infancy period, data collected among contemporary descendants of hunter-gatherers indicate that teaching and over-imitation become firmly established during childhood (Hewlett et al. 2011; Nielsen & Tomaselli 2010). Other social-cognitive traits Vaesen links to tool use, such as theory of mind (Wellman et al. 2001) and mental time travel (Suddendorf et al. 2011), are similarly established in this period – as is the uniquely human propensity for pretending, an endeavor in which the mind can find a rich bed to sow the seeds of invention (Nielsen 2012). The emergence of childhood as a life stage therefore presents itself as a critical step in the evolution of human tool use. It might also have underpinned marked increases in tool innovation among our hominin ancestors.

Vaesen alludes to the apparent lack of cumulative culture evident in the Acheulean Industrial Complex, which appeared on the paleolandscape ~1.6 mya, exemplified by the teardrop-shaped bifacial hand axes made by *Homo ergaster* and *Homo erectus*. The production of these lithic artifacts is characterized by a regularity of design that lasted for hundreds of millennia and is thought indicative of a general lack of technological innovation (Foley & Lahr 2003; Hill et al. 2009). There is evidence to suggest that such lack of innovation is due to the absence of a childhood period. During the last three decades, the most

common method used to address questions of hominin growth has been the study of fossil teeth, with a modern human-like sequence of dental development now regarded as one of the diagnostic hallmarks of our species (Dean et al. 2001). Microscopic analysis of growth patterns in fossil teeth indicates that dental development in lower Paleolithic hominins followed a chimpanzee-like timing. That is, childhood as a life stage was not present before 1.5 mya. Crucially, evidence points to a lack of childhood in hand axe–making *erectus* (Dean 2000; Dean et al. 2001). Conversely, and though a matter of ongoing debate (see Smith et al. 2010), rates of dental development found in fossilized Neanderthal teeth are suggestive of a childhood in this species (Macchiarelli et al. 2006). This ties in with the emergence of the Mousterian tool kit around 300,000 years ago that signified an order-of-magnitude increase in technological complexity that we have not looked back from.

Human offspring are confronted with a vast array of tools they must learn to use. Childhood emerged at some point in our evolution and provided time for the acquisition of the requisite skills to do so, along with the emergence of the multifarious social and cognitive advances that make us who we are. With childhood there is no need to redefine tool, redefine Man, or accept chimpanzees as humans. With childhood we became *Homo faber* (Bergson 1911/1998).

What exists in the environment that motivates the emergence, transmission, and sophistication of tool use?

doi:10.1017/S0140525X11002056

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Abstract: In his attempt to find cognitive traits that set humans apart from nonhuman primates with respect to tool use, Vaesen overlooks the primacy of the environment toward the use of which behavior evolves. The occurrence of a particular behavior is a result of how that behavior has evolved in a complex and changing environment selected by a unique population.

In his target article, Vaesen attempts to find a set of intrinsic cognitive traits, often described in terms of neurological structures, that help explain the divergent paths with respect to tool use taken by humans and non-human primates. The emphasis here seems to be skewed in the direction of intrinsic traits at the expense of ecological contexts. Yet, as Rosen (2000) pointed out succinctly, a function of an organism can never be understood in terms of its internal structure, because "a function requires an external context; a structure does not" (p. 25). I do agree with Vaesen that "no individual cognitive trait can be singled out as the key trait differentiating humans from other animals" (sect. 1). However, it is not that multiple cognitive traits differentiate humans from nonhuman primates, but that species are never adequately differentiated by means of such essentialistic criteria (Ghiselin 1974; Reed 1996).

The examples that illustrate the inadequacy of the assumption of simple mapping between intrinsic traits and functional behavior range from the convergence of nut-cracking behavior in extant primate species, where both 45-kg chimpanzees (*Pan troglodytes*) and 3-kg capuchin monkeys (*Cebus libidinosus*) use stone hammers around 1 kg in mass (Haslam et al. 2009), to upland geese with webbed feet that never go near the water. The latter were observed by Darwin (1859), who remarked, "habits have changed without a corresponding change of structure" (p. 186).

In human evolution, the time gap between the start of stone flaking and the earliest *Homo* fossils suggests that earlier hominin taxa (i.e., *Australopithecus*) could be the makers of the earliest stone tools (McPherron et al. 2010; Plummer 2004), whose relative brain sizes appear to be roughly equivalent to those of the extant great apes (Asfaw et al. 1999; Kappelman 1996). Recent discovery of 1.76-million-year-old early Acheulean tools, which pre-date the oldest known out-of-Africa hominin sites with no such artifacts, provides evidence that at least two contemporaneous hominin groups coexisted in Africa at that time: one with early Acheulean technology who remained in Africa and the other without such technology who developed strategies for dispersion into Eurasia (Lepre et al. 2011). Whether this indicates the cultural disparity within species or the existence of separate species is unknown, but I seriously doubt that such division can be caused by the preceding changes in their "cognitive" capacities alone.

Today, there is increasing evidence to suggest that changes in behavior that establish a new environmental relationship often antedate genetic, physiological, or morphological changes; and behavior is viewed as one of the leading edges of evolution, rather than simply the end product of it (Gottlieb 2002; Plotkin 1988). The recurrence of new environmental relationships may influence the selection pressures on species, favoring individuals with phenotypes that match the usage of novel behavioral resources of the environment (Lewontin 2001; Odling-Smee et al. 2003). A consensus among researchers holds that novel behavioral shifts associated with the discovery of conchoïdal fracture, which allowed for meat and marrow procurement by means of sharp-edged tools, played instrumental selective roles during human evolution (Asfaw et al. 1999; Bril et al. 2010; Isaac 1976; McPherron et al. 2010; Roche 2005; Semaw et al. 1997; Stout et al. 2010).

Our own experimental study on this particular way of exploiting behavioral resources in the environment – the control of conchoïdal fracture in flaking through direct hard-hammer percussion – revealed the necessity of considerable amount of experience in predicting and controlling the consequence of a strike given to a core (Nonaka et al. 2010). This requires seeking out the relevant features in the surface structure of the core that reflect the constraints of conchoïdal fracture. Specifically, modern experienced stone knappers have discovered a regularity that exists in the relationship between the observable layout of surfaces of the core, size of a detachable flake, and threshold of kinetic energy required to initiate the fracture, which was demonstrated by the selection of striking location and the control of movement. Essential to the acquisition of this kind of skill is the firsthand experience to explore the properties of a core and a hammer stone. We suggested that the evidence of precise control of conchoïdal fracture in the Early Stone Age records (e.g., Delanges & Roche 2005) may be indicative of the recurrence of a situation in which juveniles are provided with the experience of rediscovering important affordances of the environment directly, by looking at the surface of the core and wielding the hammer stone.

Vaesen does rightly emphasize the role of social learning in human technological accumulation. However, what exists in the environment (outside of the head) that "motivates" the accumulation of knowledge across generations is largely left out of his account. Among the nut-cracking populations of wild chimpanzees, for example, the same stone tools have been re-used over successive generations (S. Hirata and S. Carvalho personal communication). Capuchins are known to accumulate stones that are appropriate for the nut-cracking task at sites with appropriate anvils, the remains of which may last for millennia (Visalberghi et al. 2007). In such cases, not only the ecological "givens" but also the ecological "takings" and "makings" make up the facts

of the physical world that surrounds evolving populations of animals (Reed 1996). These facts of the environment are no less biological and no more cultural than neurological structures and genes are, which are equally incorporated into, and thereby contribute to, the furtherance of various biological processes of animals.

What makes a particular behavior such as tool use occur as it does is a result of how that behavior has evolved in the environment, selected and modified by a unique population (Gibson 1986; Reed 1985). Given the primacy of the environment into which animals are born toward the use of which behavior evolves, I would welcome Vaesen's making a connection between his ideas and the following question: What exists in the environment that motivates the emergence, transmission, and sophistication of tool use?

An area specifically devoted to tool use in human left inferior parietal lobule

doi:10.1017/S0140525X11001944

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Abstract: A comparative fMRI study by Peeters et al. (2009) provided evidence that a specific sector of left inferior parietal lobule is devoted to tool use in humans, but not in monkeys. We propose that this area represents the neural substrate of the human capacity to understand tool use by using causal reasoning.

Vaesen lists nine cognitive capacities crucial to tool use in humans and discusses to what extent they are also present in the great apes. One of these capacities is causal reasoning, which, as stressed by Vaesen, does not simply involve noticing the covariance between a cause and an effect, but also allows subjects to infer a mechanism relating the two. The author concludes that current evidence suggests that this capacity is present in apes only to a modest degree. He does not indicate, however, any possible anatomical basis for this cognitive difference between apes and humans.

Recently, Peeters et al. (2009) examined the neural basis of tool use in human and non-human primates (rhesus monkeys). In a comparative fMRI study, they scanned human volunteers and untrained monkeys, as well as monkeys trained to use tools, while they observed hand actions and actions performed using tools. In both species, presentation of an action activated occipito-temporal, intraparietal, and ventral premotor cortex bilaterally. In humans, however, the observation of an action performed with tools yielded an additional, specific activation of a rostral sector of the left inferior parietal lobule, referred to as the anterior supramarginal gyrus (aSMG) tool use region. They proposed that this region, unique to humans, underlies a specific way of understanding tool actions based on the appreciation of the causal relationship between the intended use of the tool and the result obtained by using it.

That monkey parietal cortex contains only the biological hand-action observation areas need not imply that these areas cannot be modified by the training to use tools, as has been documented by Iriki et al. (1996). However, the fact that monkeys learned to use simple tools does not necessarily imply an understanding of the abstract relationship between tools and the goal that can be achieved by using them. The tool used, for example, the rake, might simply become, with training, a prolongation of the arm, as shown by the response properties of neurons recorded in the medial wall of the intraparietal sulcus.

The human aSMG region was discovered by an interaction analysis subtracting out static shape differences between the tool-use and hand-action videos. This suggests that the human area uses differences in kinematics to distinguish tool actions from biological actions. This links nicely with another species difference that has been discovered by Orban et al. (2006): The human parietal cortex is much more sensitive to visual motion than is its monkey counterpart. Some of these motion-sensitive areas, such as dorsal intraparietal sulcus anterior (DIPSA), are very close to the tool area, providing, possibly, an anatomical link with aSMG. Thus, human parietal cortex is not simply more sensitive to three-dimensional form from motion (Vanduffel et al. 2002), providing more sophisticated higher-order visual analysis capacities for guiding tool action; this cortex is also more sensitive to lower-order motion, providing the kinematics signals for the aSMG region.

Two further implications of the aSMG discovery are relevant to the present discussion. First, as commented upon by Peeters et al. (2009), the grouping of tool-related neurons in the aSMG might dramatically increase the computational power of this neuronal population. Interestingly, Vaesen discusses how causal reasoning, which we propose to be implemented in the aSMG, may be instrumental in the development of technology by increasing the cost-effectiveness of individual learning strategies. As mentioned above, the grouping of tool-related neurons is lacking in monkeys. However, these neurons might be scattered throughout the biological hand-action observation circuit and, therefore, remained unnoticed in the MR scanner. To what extent the grouping may already be present in great apes remains a topic for further experimentation. The existence, however, of such an embryonic grouping, if present, could explain some of the rudimentary cognitive abilities related to tool use in apes.

Second, the human aSMG area corresponds to regions where MR responses have been measured during pantomiming and imagining tool use (see Lewis 2006 for review). Hence, the human aSMG region is involved in both the observation of tool actions and their planning. It is, therefore, conceivable that it houses neurons with mirror-neuron–like properties (Rizzolatti & Craighero 2004) that allow for both tool use and tool-use understanding. This may support tool imitation and learning by imitation. A word of caution is of course needed, as the presence of mirror neurons has yet to be demonstrated in aSMG, and their presence is a necessary but not sufficient condition for imitation to develop.

In conclusion, with the proviso that Peeters et al. (2009) studied rhesus monkeys and not great apes, their findings are in striking agreement with the review of Vaesen and provide a neuronal basis for species differences in eye-hand coordination and in causal reasoning related to tool use.

Foresight, function representation, and social intelligence in the great apes

doi:10.1017/S0140525X11002068

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Abstract: We find problems with Vaesen's treatment of the primatological research, in particular his analysis of foresight, function representation, and social intelligence. We argue that his criticism of research on foresight in great apes is misguided. His claim that

primates do not attach functions to particular objects is also problematic. Finally, his analysis of theory of mind neglects many distinctions.

Although we believe that a list of cognitive capacities involved in human tool use might be fruitful in other respects, we fail to see the gain from using it in the perspective of comparative cognition. Vaesen's list has been reverse engineered from modern human cognition. How does it help us to describe the evolution of human tool use to know whether or not a modern chimpanzee has a similar list? Vaesen claims that the list can at least explain the discrepancy between chimpanzee and human tool use. This may be, but no cognitive capacities need invoking to argue that humans and, for example, chimpanzees use tools differently. The paper could have been an analysis of the cognitive capacities themselves, or a paper on the evolution of human technology – but using a comparative approach does not tie the paper together.

We also find problems with Vaesen's treatment of the primatological research on cognitive capacities per se. Specifically, we want to comment on the analysis of foresight, function representation, and social intelligence.

Vaesen regards a study by Osvath and Osvath (2008) on chimpanzees and orangutans as coming closest to showing inhibition in relation to foresight in nonhuman primates. One of the study's four experimental conditions included an inhibition task where the subject could select either an immediate, favoured reward (a grape) or a tool that might be used 70 minutes in the future for retrieving a large, also highly favoured liquid reward (rosehip berry soup). All subjects performed significantly above what would be expected of an animal with no foresight. However, Vaesen dismisses the results as a consequence of mere associative learning, based on the misapprehensions of Suddendorf and Corballis (2009) in their commentary on the study. Not only does the original study contain an experiment specifically designed to control for associative learning; there also exists an extensive response to Suddendorf and Corballis (Osvath 2010) that Vaesen does not account for. There is little doubt that the inhibitory behaviour was not caused by purely associative learning.

Vaesen does, for sake of argument, suppose that associative learning can be excluded; but he then finds that the different rewards are not qualitatively different, which would imply that the apes are not taking a future state into account when selecting their tool. Vaesen argues that wanting to eat a grape and wanting to drink rosehip berry soup are the result of the same desire: namely, hunger.

First, hunger is not a desire; it is a response to a physiological state. In any case, the subjects in this study were not particularly hungry or thirsty: Their daily feeding routines had not been interrupted. Second, eating and drinking are dissimilar activities, with different physiological outcomes. For the time being, allow the most parsimonious interpretation to be that the apes select between two different desires.

Vaesen concludes from very few studies – two, it appears – that great ape foresight is highly limited compared with that of humans. However, the few great ape studies that exist simply have not tested for a range of foresight skills allegedly present in humans. Much work needs to be done before great ape foresight abilities can be delineated. We are plainly ignorant of significant facts about great ape foresight and also know little about the mechanisms of foresight in themselves. If a certain, uniquely human type of foresight is indeed essential for superior tool use, the evidence for such uniqueness, in the experimental literature that Vaesen cites, is insufficient.

Third, we have concerns with how Vaesen handles the abilities of great apes to represent tool function. We will here limit ourselves to the previously mentioned foresight study by Osvath and Osvath (2008). The fourth experimental condition in that study included novel items from which the apes were to select. Of the four items, only one was functional for retrieving the future reward. The subject had to decide, by visual inspection of each novel item, whether that item would be functional in the future. Stimulus generalisation – of length, colour, size, and shape – was precluded. The apes performed significantly above chance.

It is difficult to explain these results without ascribing to the apes some representation of function. This novel use would imply a type of causal understanding, according to Vaesen's line of argumentation. When it came to ascribing to a tool a particular function, it is obvious that, in the other three conditions in the study, the apes consistently chose the functional tool. The experimental condition for associative learning controlled more specifically for whether the tool was selected because of its function – rather than representing an arbitrary, reinforced stimulus. These results are not compatible with Vaesen's statement that primates do not attach particular functions to particular objects.

Fourth, Vaesen adopts Premack and Woodruff's (1978) characterization of *theory of mind* in the section on social intelligence. Since this definition was first proposed, the capacity for theory of mind has been shown to consist of several components (e.g., Call & Tomasello 2008; Gärdenfors 2001; 2003). One should at least distinguish understanding the emotions of others from understanding their attention, understanding their intentions, and understanding their beliefs. Only the last capacity is normally called a *theory of mind*. With the other capacities, it is fully possible for the agent to react to visible behaviours directly. Evidence for both the capacity to understand emotions and the capacity to understand attention *can* be found in non-human primates (Preston & de Waal 2002; see Call & Tomasello 2008). The situation is less clear for understanding intentions, although Tomasello et al. (2005) claim the capacity to form *joint intentions* as the hallmark of humans. Only with respect to understanding the beliefs of others is there, so far, no evidence from nonhuman primates. A less anthropocentric research methodology might change the situation, as it did for research on understanding the attention of others.

Look, no hands!

doi:10.1017/S0140525X1100207X

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Abstract: Contrary to Vaesen's argument that humans are unique with respect to nine cognitive capacities essential for tool use, we suggest that although such cognitive processes contribute to variation in tool use, it does not follow that these capacities are *necessary* for tool use, nor that tool use shaped cognition per se, given the available data in cognitive neuroscience and behavioral biology.

Enhanced hand-eye coordination, social learning, teaching, language, and social intelligence undoubtedly contribute to the accumulation of advanced, human-like technologies, but are they *required* for tool use? For example, given the strong selection pressure for successful foraging, fine motor control over one's feeding apparatus, be it beak, trunk, or claw, may promote tool use (e.g., Kenward et al. 2006). Primates use their hands extensively while foraging, but many species lack hands (or analogs) yet regularly use tools. In fact, primate tool use accounts for only about 10% of documented cases of animal tool use (Bentley-Condit & Smith 2009). Furthermore, most tool-using animals do not, as far as we know, socially learn the behavior or possess other components of social intelligence deemed essential by Vaesen (e.g., Brockmann 1985).

Although Vaesen's nine capacities provide mechanisms for tool use transmission, maintenance, and improvement, thereby advancing technology, they are not preconditions for tool use as such. Therefore, although human technological achievements are unique, Vaesen's capacities and tool use itself may not be.

Studies of behavioral trait evolution demand an appropriate comparison group (i.e., all hominoidea, all anthropoidea, or all primates), but surveying analogous behaviors in distant taxa can elucidate the ecological and evolutionary contexts of these traits. Vaesen focuses on great ape studies that support his claims and ignores conflicting data. He extensively refers to the (phylogenetically distant) monkey literature that suits his argument (e.g., Cummins-Sebree & Fragaszy 2005; Hauser 1997) and ignores relevant monkey and even ape studies that do not (e.g., Hauser et al. 2002; Santos et al. 2003; Whiten et al. 2005; although Whiten et al. 2005 is mentioned later in a different context). In fact, Whiten et al.'s (2005) study and a new study (Hanus et al. 2011) may very well indicate functional fixedness in chimpanzees. The ape studies Vaesen does mention here are placed in Note 14, and one (Carvalho et al. 2009) provides a strong case of tool reuse.

Among more distant taxa, bottlenose dolphins in Shark Bay, Australia, reuse basket sponge tools for a little more than an hour, as presumably during that period the tool remains functional; but much beyond that, functionality is lost and the tool is discarded (Patterson & Mann 2011). Furthermore, functional fixedness is not necessarily a valuable cognitive trait and may even be inhibitory (e.g., Hanus et al. 2011). Flexibility, on the other hand, is a cognitive bonus, as with little to no modification a single tool becomes many (e.g., chimpanzees use sticks to fish for termites, honey [Fay & Carroll 1994], and ants [McGrew 1974] and even as hunting spears [Pruetz & Bertolani 2007]). When discussing executive control and forethought, Vaesen focuses on ape studies by Osvath and Osvath (2008) but fails to mention other ape research (e.g., Biro & Matsuzawa 1999; Boesch 1994; Boesch & Boesch 1989; Dufour & Sterck 2008; Noser & Byrne 2010; Osvath 2008). Vaesen does mention two additional studies, but again they are buried, in Note 20 rather than in the main body of his text. In fact, conflicting literature is repeatedly placed in notes (e.g., hand-eye coordination [5], functional representation [14], executive control and forethought [20], heuristics for selecting models for social learning [29], and food sharing [31]).

While not implicitly stating it, Vaesen strongly implies that human tool use and his nine capacities coevolved. If so, then Vaesen must address whether the phenotype was selected for and whether its current utility is the same as its historic use (Gould & Lewontin 1979). Human technology is obviously indicative of higher cognitive ability, but may be a product of our cognition rather than the selective force behind it. Two other well-established brain evolution theories deserve consideration: the social brain hypothesis (Byrne & Whiten 1988; Dunbar 1998) and the ecological complexity hypothesis (Reader & Laland 2002). Although tool use likely played a role in our cognitive evolution, either as a product or as a driving factor, it demands a systematic and comprehensive approach.

Finally, most of Vaesen's arguments rely on a lack of evidence, rather than evidence of absence (de Waal & Ferrari 2010). This amounts to trying to prove the null hypothesis, a nearly futile task when comparing across taxa because of (1) a lack of data for some species, (2) low ecological validity, (3) poor internal validity due to poorly designed tasks, (4) biases in research effort, and (5) the sheer difficulty of researching cognition in animals. Vaesen even admits, but is not deterred by the fact, that for 8 of the 16 traits he claims are decidedly more pronounced in humans than in chimpanzees, few data are available (Table 2).

Tool use should be studied with a comparative approach, including the examination of other taxa and analogous behaviors, and by maintaining an appreciation for the ecological and social contexts in which tool use arises (de Waal & Ferrari 2010). For example, Povinelli's studies on captive chimpanzees using human behavioral models fail to show causal reasoning (but see Call 2010), whereas Cheney and Seyfarth's (1995) study with wild baboons, which uses more relevant tests, seems to demonstrate causal reasoning in natural social contexts. With more appropriate tests, apes may very well excel (albeit, not to the level of humans) in all of the nine capacities. Non-primates, such as rats, crows, and likely elephants, show causal reasoning (Blaisdell et al. 2006; Plotnik et al. 2011; Taylor et al. 2009a).

Other areas that could benefit from this comparative approach include, but are not limited too, imitation (e.g., dolphins; Herman 2002), social learning (e.g., woodpecker finches; Tebbich et al. 2001), social intelligence (e.g., dolphins; Connor 2007), insight learning (e.g., crows; Taylor et al. 2010), forethought (e.g., dolphins; McCowan et al. 2000), teaching (e.g., meerkats; Thornton & McAuliffe 2006), inhibition (e.g., rodents, birds, and marine invertebrates; Dally et al. 2010; Kim 2010; Vander Wall et al. 2009), food sharing (e.g., killer whales; Ford & Ellis 2006), and theory of mind (e.g., dolphins and elephants; Douglas-Hamilton et al. 2006; Plotnik et al. 2010; Xitco et al. 2004).

Surely those without hands deserve another look.

So, are we the massively lucky species?

doi:10.1017/S0140525X11002159

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Abstract: We are in vehement agreement with most of Vaesen's key claims. But Vaesen fails to consider or rebut the possibility that there are deep causal dependencies among the various cognitive traits he identifies as uniquely human. We argue that "higher-order relational reasoning" is one such linchpin trait in the evolution of human tool use, social intelligence, language, and culture.

We are in vehement agreement with most of Vaesen's key claims. We have long argued that sophisticated tool use and abstract causal reasoning reflect a fundamental cognitive discontinuity between humans and all other extant animals (Penn & Povinelli 2007a; Penn et al. 2008; Povinelli 2000). And we have previously proposed, in this very journal, an explanation for the discontinuity between human and non-human minds that overlaps with Vaesen's in many respects (Penn et al. 2008).

The remainder of this commentary, then, should be read as an intramural critique. We have a couple of small issues with Vaesen's argument and one big one.

Causal reasoning. Vaesen correctly points out that "causal understanding involves more than just noticing (e.g., through trial and error) the covariance between a cause … and an effect" (sect. 4, para. 1). But then Vaesen goes on to claim, incorrectly in our view, that a cognizer must "infer a mechanism" in order to possess true causal understanding. To be sure, there are those who have advanced such a view (e.g., Ahn et al. 1995). However, the notion that prior knowledge of a mechanism is required for causal understanding offers no insight into how causal learning can get started: that is, how can a reasoner infer a *causal* mechanism from *noncausal* observations (Cheng 1993; 1997)? More recent theoretical work based on variants of causal Bayes nets has established that a cognizer can recognize a relation as specifically causal without necessarily understanding anything about unobservable

causal mechanisms (for reviews see Gopnik & Schulz 2007; Holyoak & Cheng 2011).

Because Vaesen overlooks the distinction between causal reasoning and the representation of unobservable causal mechanisms, he misconstrues the results of Povinelli's rake experiments as evidence that chimpanzees learn through "associative learning" (sect. 4, para. 3). We have argued that the chimpanzees in these experiments were perfectly capable of first-order causal understanding (Penn & Povinelli 2007a). It is the ability to reason about higher-order causal relationships that eludes them (Penn et al. 2008; Povinelli 2000).

Function representations. Vaesen is probably correct that chimpanzees do not form "functional representations" (sect. 5) of tools in the same manner as humans. But it seems implausible to us that chimpanzees do not form functional representations at all. They certainly perceive stick-like objects as able to "function" in a certain manner for achieving certain goals, and these representations generalize over a fairly wide variety of shapes, colors, and textures. In our view, chimpanzees are perfectly able to form functional representations of stick-like objects in terms of surface features of the objects – they just fail to represent "functions" in terms of the underlying causal mechanisms involved (Povinelli 2000).

Explaining the discontinuity. In summarizing his findings from the first half of the paper, Vaesen (sect. 11) argues that "no individual cognitive trait" can be singled out as the key trait differentiating humans from other animals, and then claims that his argument is an antidote to "single-trait explanations of 'humaniqueness'" (sect. 11, para. 3). This is our major point of contention with Vaesen.

To be sure, we know of no researcher who claims that there is one and only one trait that distinguishes human and nonhuman cognition. There are, indeed, a large number of cognitive traits that appear to be distinctively human – ranging from mental state attribution and language to causal reasoning and contingent cooperation. But Vaesen does not consider or rebut the possibility that there might be a deep dependency between many or even all of these disparate traits both at a cognitive/computational level of explanation and at an evolutionary/biological level of explanation.

It is possible, of course, that each of our uniquely human cognitive traits evolved independently of each other, and that each is embodied in a separate and independent "module" in the human brain. There are certainly researchers who defend such a "massively modular" explanation for human cognition (Carruthers 2005; Tetzlaff & Carruthers 2008). But to our eyes, it seems wildly implausible that one and only one species was lucky enough to have evolved separate and independent mechanisms for each of these uniquely human traits (in a few million years to boot), whereas no other species evolved any of them. It seems much more likely (not to mention parsimonious) that there are deeper dependencies among these disparate traits such that a species that evolved a few linchpin traits would be in a more propitious state, from an evolutionary point of view, to acquire the others.

We have argued that the ability to represent and reason about the relation among relations – that is, "high-order relational reasoning" – is a plausible candidate for one of these linchpin traits (Penn et al. 2008). It certainly seems noteworthy that many of the cognitive traits Vaesen identifies as instrumental in the evolution of human tool use – causal reasoning, functional representations, foresight, teaching, mental state attribution, contingent reciprocity, goal sharing – appear to depend upon a common set of higher-order relational competences.

Numerous researchers, for example, have demonstrated a strong empirical relationship between higher-order relational reasoning and theory-of-mind competence (e.g., Andrews et al. 2003; Zelazo et al. 2002). And almost all theoretical models of mental state attribution presume higher-order relational reasoning as an underlying mechanism (e.g., see the theories proposed in Carruthers & Smith 1996). With respect to causal reasoning, most contemporary researchers agree that the ability to reason about a *network* of causal relations in a systematic and allocentric fashion is the bedrock of human causal cognition (e.g., Lagnado et al. 2005; Tenenbaum et al. 2006). Higher-order relations are also central to language (e.g., Gomez & Gerken 2000; Hauser et al. 2002; Pinker & Jackendoff 2005).

The cognitive traits Vaesen subsumes under the heading of "executive control" are a motley set. There is good evidence that some of these – e.g., inhibition, autocuing, and self-monitoring – are necessary components of the ability to reason about higher-order relations (Andrews et al. 2003; Cho et al. 2010; Halford et al. 1998; Robin & Holyoak 1995). Others – for example, foresight, hierarchical planning, and inferential coherence – are plausibly the *result* of being able to reason about higher-order relations.

Much work remains to be done to disentangle the necessary and sufficient components of higher-order relational reasoning in humans, and to understand how such a unique computational mechanism evolved in the brain of one particular species. However, there is already strong evidence, from a wide variety of domains and researchers, that this ability lies at the heart of "what makes us so smart" (Gentner 2003). Our principle difference with Vaesen is that he neither considers nor rebuts this possibility.

The key to cultural innovation lies in the group dynamic rather than in the individual mind

doi:10.1017/S0140525X11002081

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Abstract: Vaesen infers unique properties of mind from the appearance of specific cultural innovation – a correlation without causal direction. Shifts in habitat, population density, and group dynamics are the only independently verifiable incentives for changes in cultural practices. The transition from Acheulean to Late Stone Age technologies requires that we consider how population and social dynamics affect cultural innovation and mental function.

By focusing on human cognitive capabilities, Vaesen dismisses the function of the group dynamic in the emergence of complex social repertories (Garrod & Doherty 1994; Steels 2006; Steels et al. 2002). Underlying biological capacities tend to be difficult to delineate; the same biology often displays considerable behavioral flexibility in response to shifts in social dynamics and environmental challenges. Vaesen's nine cognitive prerequisites are important for human cultural evolution, but one can make only educated guesses about how, why, or when these capabilities emerged. Evidence for cognitive capacities is inferred from the presence of the tool assemblages they purport to explain, without independent evidence for the direction of causation. Certainly, one can argue that many if not all of these capacities, including language, were present in *Homo erectus* toolmakers.

Three parameters are consistently associated with complex cultural adaptations to an environment: (1) relatively large brains and prolonged postnatal, activity-dependent maturation of the central nervous system, (2) environmental stress, and (3) increased population densities. Over hominin evolution, as a consequence of maturational delays and encephalization, human brains came to have remarkable developmental plasticity throughout the lifespan. Changes in life history created the potential for behavioral flexibility and altered social dynamics among mothers, infants, and others (Hrdy 2009; Kaplan et al. 2000; O'Connell et al. 2002; Ragir 1985). Evidence for

maturational changes is abundant in the fossil record beginning 3–4 mya and indicates a relatively modern profile of prolonged juvenile growth and encephalization beginning with *H. erectus* (Ragir 2000). The altered human life history is best explained through changes in habitat, diet, and locomotion (Aiello & Wells 2002; Cachel & Harris 1995; Laden & Wrangham 2005; Ragir et al. 2000). The transition from Acheulean to Middle Palaeolithic in Europe (Middle Stone Age in Africa) took place long after the appearance of a human-size brain and developmental profile. This leaves the interdependence between environmental stress and regional population growth as the incentive for the proliferation of human technologies in the Middle Pliestocene.

Improvements in diet supported increases in population densities by decreasing birth spacing (Aiello & Key 2002). Intensification of exploitation of local resources has been closely associated with a division of labor and the specialization of knowledge required for rapid technological advancement (Jochim 1981). Technological advancement progresses slowly where populations are small and widely dispersed, and where there is little external pressure for change, as in modern hunter-gatherer societies (Jochim 1976); indeed, technological advances may be lost between generations when there is a drop in population density (Boserup 1981).

Let us consider how changes in population density result in the specialization of labor and knowledge using cooking as an example. Within a community, cooking skills are typically widespread, but the quality of production is uneven. In small communities, foods are often limited to local produce and ethnic tradition, and equipment is general purpose. Among home cooks, some are especially talented and capable of producing high-quality meals, but their innovative recipes and techniques often disappear after a generation or two. As communities increase in size, functional institutions appear (e.g., courts, estates, the army) that use full-time cooks to prepare meals for dozens of people. Professionals design specific tools to take the guesswork out of combining ingredients and systematize the techniques and timing of food preparation. With specialization comes a formal transfer of skills in the form of recipes, apprenticeships, and schools that disseminate a standardized knowledge of cooking methods. Archaeologically, the simple artifacts of home cooking appear as early as sedentary villages; and these continue to be found even after the appearance of the specialized toolkits of professional chefs. One does not supersede the other – they continue, one changing slowly and the other proliferating innovations, spatially but not temporally distinct.

Studies of language formation offer further insights into the emergence of complex cultural repertories. Among deaf individuals, the effect of community size on the emergence of communication systems from home sign to fully developed sign languages demonstrates the centrality of social dynamics. Isolated deaf children invariably use gestures to communicate with family members and achieve a perceptible degree of systematization in their gestural repertories (Goldin-Meadow 2003). However, within a broader community, systemization creates stable, broadly shared system of signs (Kendon 1984). Given a community open to new learners, the informal syntax of a pidgin coalesces into a formal syntactic system within a few generations (Kegl et al. 1999). Whereas isolated deaf children create idiosyncratic conventions in interaction with their families, global conventions emerge only within communities of some critical size (Ragir 2002; Senghas et al. 2005).

Simulations and experimental studies further demonstrate the role of collaborative learning in the proliferation and maintenance of novel systems of information exchange. Fay, Garrod, and colleagues (e.g., Fay et al. 2010; Garrod et al. 2010) compared the emergent graphic communicative systems of those participants engaged in pair-wise interactions with different group members and those of isolated pairs over an equivalent number of communicative turns. Only in the case of community-wide interactions did individuals converge on a global system. Furthermore, global signs were found to be more transparent with respect to meaning than were those produced by isolated pairs (Fay et al. 2008). These results suggest that system standardization and streamlining may require collaborative negotiations among members of groups larger than a family (Fay et al. 2000).

Group dynamics lead to the emergence of conventional procedures and global symbols, in such domains as ceramics, fashion, music, and the Internet, from cottage crafts to the assembly line. The resultant technologies alter the ontogeny of individual minds, in the form of activity-dependent changes in information processing (Bavelier et al. 2010; Donald 1991; Greenfield 1984; Tobach et al. 1997). Simple negotiations of information are capable of producing unexpectedly complex behavioral repertories, such as seen among social insects, migratory birds, and animals engaged in cooperative parenting (Hrdy 2009). Social interactions that systematize activities and negotiate global conventions effect significant changes in neural connectivity and cognitive functions. Unique human faculties are likely to emerge as the result of, rather than as necessary conditions for, innovative cultural repertories.

The limits of chimpanzee-human comparisons for understanding human cognition

doi:10.1017/S0140525X11002093

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Abstract: Evolutionary questions require specialized approaches, part of which are comparisons between close relatives. However, to understand the origins of human tool behavior, comparisons with solely chimpanzees are insufficient, lacking the power to identify derived traits. Moreover, tool use is unlikely a unitary phenomenon. Large-scale comparative analyses provide an alternative and suggest that tool use co-evolves with a suite of cognitive traits.

We are sympathetic to Vaesen's view that no single cognitive trait differentiates human tool behavior from that of other animals, and we agree that comparative analysis has an important role in understanding the cognitive bases of human tool use. However, in our view, several vital issues are unaddressed. Have tool-using capacities driven human cognitive evolution, or is tool use the by-product of another ability? To what degree are the perceptual and cognitive traits underlying tool use and technological cultural evolution independent from each other and from morphological, societal, or ecological traits? What is the role of culture and development in shaping patterns of tool innovation and social learning? How much of cumulative cultural evolution rests on increases in causal understanding of tools, as Vaesen suggests, and how much on retention of "blind" variants (Simonton 2003)?

Here we focus on problems raised by the analysis of human tool behavior based on comparisons with one taxon, chimpanzees. Vaesen's aim is not to compare humans and chimpanzees, but to understand the cognitive bases of human tool use. As useful as comparisons with chimpanzees are, Vaesen's application of this tactic is critically flawed for at least four reasons. Although Vaesen admits his narrow focus on chimpanzees, the flaws are germane both to his conclusions and to other work in the field.

First, Vaesen's chimpanzee-human comparison assumes that shared ancestry explains similarities, whereas differences are explained by independent evolution of the trait in humans and not, for example, the loss of the trait in chimpanzees. However, the ancestral state must be established, which requires investigation of additional species (de Kort & Clayton 2006).

Second, tool use is unlikely a unitary phenomenon. A variety of neurocognitive and genetic mechanisms can underlie a behavioral outcome such as tool use (Shumaker et al. 2011). Hence, it is not a given that similarities and differences between species in tool-related behavior or test performance equate to similarities and differences in underlying cognition, potentially compromising the explanatory power of species comparisons. Independent evolution may have produced similar behavioral specializations with different underlying mechanisms (de Kort & Clayton 2006), or behavioral similarities may appear as a consequence of some third variable, such as enhanced social tolerance (van Schaik et al. 1999). Furthermore, tool-using capacities may be present but unexpressed. For example, expression of true and proto-tool use (Shumaker et al. 2011) appears sensitive to variation in social and ecological conditions. Finches turn to tools in arid conditions, rarely using tools to extract prey where food is abundantly accessible (Tebbich et al. 2002); dolphins use sponges to locate prey that cannot be detected by other means (Patterson & Mann 2011); adult male capuchin monkeys are strong enough to bite open certain nuts, whereas females and juveniles require tools to open them (Fragaszy & Visalberghi 1989); and grackles use water to soften hard food when the risks of kleptoparasitism are low (Morand-Ferron et al. 2004). These observations suggest tool use may frequently be a costly option employed flexibly, taken when other options fail or are unavailable. Similarly, innovation in tool use can be employed flexibly; for example, driven by the social milieu (Reader & Laland 2003; Toelch et al. 2011). Hence, numerous variables could underlie species differences in tool-related behavior, and even apparent similarities may reflect different underlying mechanisms.

Third, chimpanzees may be well studied, and our close relatives, and provide much informative data (e.g., Hrubesch et al. 2009; Marshall-Pescini & Whiten 2008), but other animals provide relevant data and counterpoints to Vaesen's proposals. For example, work on finches and crows demonstrates that social learning is not essential for the acquisition of tool use (Kenward et al. 2005; Tebbich et al. 2001); meanwhile macaque observational data suggest that social transmission of nonfunctional object manipulation occurs outside humans (Leca et al. 2007, who do not class nonfunctional behavior as tool use). Similarly, selective social learning may be rarely documented in apes but has been described in numerous other species, including monkeys, other mammals, fish, and birds (Laland 2004; Lindeyer & Reader 2010; Seppänen et al. 2011; van de Waal et al. 2010). Selective social learning may be necessary for cumulative cultural evolution, but is clearly not sufficient, unless cumulative cultural evolution occurs unobserved in these animals. Researchers have demonstrated several other behaviors in non-primates that Vaesen identifies as distinctively human: ants, pied babblers, and meerkats teach; fish punish and image-score; birds use baits to trap prey, forgoing immediate rewards in a manner not unlike the human traps that Vaesen argues require foresight and inhibition (Bshary & Grutter 2005; 2006; Shumaker et al. 2011; Thornton & Raihani 2011). We urge caution in interpreting even flexible and sophisticated tool use as necessarily the product of complex cognition.

Finally, any comparison based on an effective sample size of two is problematic. Humans and chimpanzees differ on numerous characteristics. In the absence of additional behavioral data on the role of underlying candidate mechanisms in tool use, any of these characteristics alone or in combination could account for differences in tool behavior. To robustly identify correlates of tool use with comparative data, repeated and independent co-evolution must be observed, using modern techniques to focus on independent evolutionary events and to account for multiple confounding variables (Nunn & Barton 2001). Confidence in such results is strengthened further if the same patterns are observed in multiple taxa. Such correlational comparative analyses, incorporating large numbers of species, reveal that avian and primate tool use has co-evolved with several cognitive traits and with brain volume measures, and (in primates) with manual dexterity (Byrne 1997; Deaner et al. 2006; Lefebvre et al. 2002; 2004; Overington et al. 2009; Reader & Laland 2002; Reader et al. 2011; van Schaik et al. 1999). These data, supported by discoveries of tool use capabilities in species previously not noted tool users (Reader et al. 2011; Shumaker et al. 2011), are consistent with the idea that tool use can result from a generalized cognitive ability and that it forms part of a correlated suite of traits. However, such analyses would benefit from experimental data teasing apart the processes underlying tool behavior.

If human tool use really is unique, identification of its cognitive bases by comparison with any species will be problematic. We must unpack tool use, understand the underlying motivational and neurocognitive mechanisms in humans and other species, and study a range of species that both possess and lack these abilities in order to understand the consequences for tool behavior. Evolutionary approaches hence have an important role to play in investigations of cognition. Work with chimpanzees is but one part of solving this important issue.

ACKNOWLEDGMENTS

We gratefully acknowledge funding by the Netherlands Organisation for Scientific Research (NWO) Cognition Programme, the NWO Evolution and Behaviour Programme, and Utrecht University's High Potentials fund.

The dual nature of tools and their makeover

doi:10.1017/S0140525X11002135

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Abstract: Vaesen argues that functional knowledge differentiates humans from non-human primates. However, the rationale he provides for this position is open to question – with respect to both the underlying theoretical assumptions and inferences drawn from certain empirical studies. Indeed, there is some recent empirical work that suggests that functional fixedness is not necessarily uniquely human. I also question the central role of stable function representations in Vaesen's account of tool production and use.

In his target article, Vaesen acknowledges the fundamental role of tools in characterizing uniquely human psychological skills, but he perseveres with a vision that distinguishes material tools from psychological (ideal) ones. The argument he develops in the article omits a long-standing and important conceptual tradition in psychology, namely the cultural-historical tradition (e.g., Cole 1996). In this approach, tools have a dual nature; they are at the same time both material and ideal. The dual nature of tools has implications for many of the nine cognitive capacities noted by Vaesen. I will focus on functional representation, as it has important implications for how we understand and develop novel forms of artifacts. Vaesen argues that functional knowledge differentiates humans from non-human primates, but his argumentation is problematic – with respect both to the *empirical evidence* and to certain of his *theoretical assumptions*, which I outline briefly below.

Problems concerning empirical evidence. There is some recent empirical evidence that seems to show that functional fixedness is *not* uniquely human. Hanus et al. (2011) have provided suggestive evidence for the hypothesis, put forward by Tennie et al. (2010), that the difference they observed between chimpanzees and orangutans in their ability to solve the Floating Peanuts task (Mendes et al. 2007) was due to the functional fixedness of the chimpanzees with respect to the water dispenser. In Experiment 3, Hanus and colleagues showed that simply adding a new water dispenser in the experimental settings led the chimpanzees to use water as a tool for recovering the peanuts – but by taking water from the new dispenser only, and not from the one from which they used to drink. This would seem to indicate that the chimps also show functional fixedness.

Theoretical assumptions. Stable function representations cannot account for the peculiar human ability to generate functions that go beyond what is physically feasible to perform with any material thing. The generation of such functions is the result of the dual nature of artifacts (material and ideal), as expressed in cultural-historical psychology (Ilyenkov 1977). Vaesen (2011) recognizes the dual nature of tools, but addresses the ideal side as representing the intentions of the designers embodied in the tool (i.e., functional aspects) as well as by other roles involved in the production of the material object (marketing, manufacturing). But the ideal component is not a matter of capturing the functional or pragmatic factors that in different moments inform the production of a material tool. It has to do rather with how people harness material things (natural and artificial, abiotic and biotic) for thought.

It has to do with two complementary sides of the same coin: on the one side, with the ability to perceive, understand, and use for their own goals the intentional relations that other persons have with an object or tool in their everyday practice – the intentional relations that other people have to the world through that object (i.e., intentional affordances; Tomasello 1999). This intentional relation may or may not be related to the intentions of the people involved in the original production of the artifacts (Rizzo 2000; 2006). Indeed, as observed by the Victorian writer Samuel Butler (1912/1951): "Strictly speaking, nothing is a tool except during use. The essence of a tool, therefore, lies in something outside the tool itself" (p. 121).

On the other side, the ideal component has to do with our capacity to go beyond what is physically feasible to perform with any material thing. This is an ability humans show very early in their development; for example, in pretend play. In pretend play, meaning is cast on objects in virtue of the actions the objects allow the children to perform, yet these actions are performed *away from* conventional use of the object. Pretend objects still need to support the pretend act, but a pretend horse does not need to afford riding or feeding; it only needs to afford pretend riding or feeding. Actually, the child can select very different objects as a pretend horse, insofar as the objects are good enough to support the specific enactment. *It's the pattern of action that specifies the meaning, not the object* (Szolonsky 2006). Lev Vygotsky (1933/1967) gave a clear description of this phenomenon:

> In play the child creates the structure meaning/object, in which the semantic aspect – the meaning of the thing – dominates and determines his behavior. To a certain extent meaning is freed from the object with which it was directly fused before. I would say that in play a child concentrates on meaning severed from objects. (p. 11)

And Vygotsky was quite explicit in stating that "a child does not symbolize in play":

> A symbol is a sign, but the stick is not the sign of a horse. Properties of things are retained, but their meaning is inverted, i.e., the idea becomes the central point. It can be said that in this structure things are moved from a dominating to a subordinate position. (p. 11)

Pretend play is most likely a uniquely human social activity (Rakoczy 2008); and, like speech, it has to do with the emancipation of situational constraints and with the creation of a new reality, which exists only in virtue of the human ability to share intentions. This allows the arbitrary creation of what Searle (1995) has named the *status function* of objects. For example, there is nothing in the physical constitution of a 10-euro note that makes it money, as even if I could clone a 10-euro note atom by atom, the result would not be money. It is the collective, yet subjective, intentionality that creates an objective and factual reality, which exists only for humans.

Therefore, specifically human functional knowledge would be better characterized not by stable function representation but by pretend play and drama inquiry. Indeed, these are just the key components of human innovative strategies such as generative scenarios (Rizzo & Bacigalupo 2004) and tinkering with things:

> Tinkering is what happens when you try something you don't quite know how to do, guided by whim, imagination, and curiosity. When you tinker, there are no instructions – but there are also no failures, no right or wrong ways of doing things. It's about figuring out how things work and reworking them. Contraptions, machines, wildly mismatched objects working in harmony – this is the stuff of tinkering. Tinkering is, at its most basic, a process that marries play and inquiry. (Banzi 2008, vi–vii)

The role of executive control in tool use

doi:10.1017/S0140525X1100210X

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Abstract: Comparing cognitive functions between humans and nonhuman primates is helpful for understanding human tool use. We comment on the latest insights from comparative research on executive control functions. Based on our own work, we discuss how even a mental function in which non-human primates outperform humans might have played a key role in the development of tool use.

Research on executive control has rapidly grown over the last 15 years. There has been an increasing conjunction of psychology and neuroscience, not only in brain imaging, but also in single-neuron studies in monkeys (Stoet & Snyder 2004; 2009).

There is general agreement that the functions involved in executive control are used to coordinate and resolve conflicts between more basic processes. There are a number of different mechanisms that are part of the executive control family: (1) *flexibility* – the capacity to switch attention between different tasks; (2) *goal setting* – the capacity to set a goal; (3) *planning*, including initiation and sequencing – the capacity to determine a series of steps necessary to reach a goal; (4) *inhibitory control* – the capacity to suppress distracting or irrelevant information and thoughts; (5) *monitoring* – the capacity to monitor whether actions result in their intended outcome; (6) *adjustment* – the capacity to adjust a course of action even after it has been initiated; and (7) *maintenance* – short-term maintenance of information related to the above functions; for example, goal setting implies that the brain can maintain the goal representation for a certain time.

Vaesen lists only some of these executive functions, namely, inhibitory control, planning, and monitoring. Further, he lists *autocueing*; that is, the capacity to think about things other than those triggered by external stimuli. This use of autocueing

was introduced by Donald (1993; cited by Vaesen), who states that animals "are creatures of conditioning, and cannot 'think' except in terms of reacting to the present or immediately past environment" (p. 146). Donald continues: "Humans alone have self-initiated access to memory, or what may be called 'autocueing'" (p. 146). The difficulty with the concept is that autocueing has not received much attention from other researchers; further, research in the past decade has unequivocally shown that animals actually use internal representations to guide the processing of external stimuli (often referred to as *endogenous control*). Such internal representations can, for example, encode which potential responses are relevant in a certain task context; and such internal representations enable animals to respond in ways that are quite different from the nature of the external stimuli. A number of laboratories have successfully recorded single neurons encoding endogenously activated action and task representations (for a review, see Stoet & Snyder 2009).

What is most important for this commentary, though, is that there is a difference in the abilities of humans and monkeys to switch between endogenously controlled task representations. Extensive research has demonstrated that monkeys are more flexible in rapidly switching between tasks than are humans, who even with long training can still not switch as rapidly as monkeys can (Caselli & Chelazzi 2011; Stoet & Snyder 2003; 2007).

Therefore, by some measures, monkeys outperform humans in mental flexibility. We hypothesize that although humans are at a disadvantage in laboratory task-switching experiments, this limited flexibility might come as an advantage for cognitive development associated with the construction and use of complex tools. (With "complex tools" we mean constructed tools.) Limited mental flexibility supports concentration. We know that humans are good at concentration. The human skill to concentrate develops mostly before the age of 10, although it seems to continue improving during adolescence. Concentration is a necessary component of long-lasting and complex tasks, some of which may have played an important survival role in prehistory, including keeping a fire burning, cooking, hunting a herd of animals for days, and designing and using complex tools. Our ability to concentrate is likely to have co-evolved with and may even have preceded our ability to use tools. Hence, a human's limited mental flexibility in comparison with a monkey's may actually be a key element in the causal chain that led to tool use.

Evidence from convergent evolution and causal reasoning suggests that conclusions on human uniqueness may be premature

doi:10.1017/S0140525X11001956

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Abstract: We agree with Vaesen that there is evidence for cognitive differences between humans and other primates. However, it is too early to draw firm conclusions about the uniqueness of the cognitive mechanisms underlying human tool use. Tests of causal understanding are in their infancy, as is the study of animals more distantly related to humans.

Imagine if we had attempted to define the uniqueness of human social cognition in the year 2000. Investigations examining primate theory of mind had started more than 30 years before. Despite this, researchers had still not developed experimental paradigms with sufficient ecological validity to thoroughly test the cognitive abilities of primates. We would have concluded that there was a large gap between human and ape social cognition. Hare et al.'s seminal work (2001), where chimpanzees were put into competitive situations rather than cooperative ones, suggests that they can take the perspective of others, though as always, this conclusion is controversial (see Vonk & Povinelli 2006). This work has been built on in the past 10 years, with a number of novel paradigms being designed, where, for example, food must be stolen from others or an ape must infer which food item another individual has eaten (see Call and Tomasello 2008 for review). Because of the high level of behavioral sophistication uncovered by these recent findings, it is now possible to make a case for the gap between human and ape social cognition being far smaller than previously thought (Call and Tomasello 2008; Schmelz et al. 2011; but see Penn & Povinelli 2007b; Penn et al. 2008).

What research on social cognition teaches us is that we have to be careful that our paradigms are sufficiently fine tuned and ecologically valid before drawing strong conclusions.

Is the trap-tube, the current paradigm predominantly used in physical cognition tests (and discussed by Vaesen in the target article), sufficient for drawing conclusions about animals? We suggest not. The trap-tube problem requires an animal to extract food from an apparatus while avoiding a trap in its surface. Slight changes to this test, such as whether an animal is allowed to pull food out of the tube, leads to differences in performance at test, and consequently, the conclusions drawn about what the animal understands (Mulcahy & Call 2006a).

Furthermore, whereas great apes do fail to transfer information between the trap-tube and trap-table tasks while using tools, the same pattern is not seen when they do not need a tool and can instead use their own finger (Seed et al. 2009). It appears, then, that the tool-use aspect of the trap-tube problem creates an additional cognitive load that interferes with problem solving. Most important, adult humans fail to solve a control condition where the trap-tube is inverted (Silva et al. 2005). Given that objects only fall down and not up, an animal that understands why the trap works should treat an upside-down trap as non-functional. In contrast, an animal that has associatively learnt to avoid the trap should continue to avoid it, irrespective of its position in the tube. Adult humans, however, make the striking error, as some animals have done (e.g., Visalberghi & Limongelli 1994), of continuing to avoid the trap when it is in the upside-down position. In contrast, apes, woodpecker finches, and New Caledonian crows do not avoid the trap in an inverted tube (Mulcahy & Call 2006a; Taylor et al. 2009a; 2009b; Tebbich & Bshary 2004).

It seems premature to draw strong conclusions about the absence of inferential causal reasoning abilities from a test that seems to be confounded by tool use and solved incorrectly by adult humans.

Claims about human uniqueness also need to consider evidence from evolutionary convergence. There is no reason why distantly related species facing similar socio-ecological challenges as humans were could not have evolved cognitive mechanisms lacked by species more closely related to humans. Imagine if we had stopped the clock in 1995 and attempted then to draw a line between humans and animals. At that point in time we would have thought that wooden hook tools, experience projection, and planning for tomorrow were capacities exclusive to humans. The reason for this is that few scientists had investigated the possibility that convergent evolution may have led birds to have evolved complex behaviors and cognition.

Today, evidence from work on the *Corvidae* family has shown that New Caledonian crows can manufacture hook tools by sculpting wood (Hunt 1996; Hunt & Gray 2004) and can spontaneously solve multi-stage metatool problems (Taylor et al.

2010), while scrub-jays have been shown to recall the past (Clayton & Dickinson 1998) and plan for tomorrow (Raby et al. 2007). In the social sphere, ravens engage in play caching to identify thieves (Bugnyar et al. 2007), and only scrub-jays with experience of stealing food engage in sophisticated cache-protection strategies (Emery & Clayton 2001). The only non-human evidence for experience projection and hook tool manufacture in the wild comes from corvids, as does the strongest evidence for future planning. Finally, although apes cannot transfer knowledge between the trap-tube and trap-table while using tools, New Caledonian crows can (Taylor et al. 2009a).

Evidence from convergent evolution, therefore, needs to be considered if we are to draw the right conclusions about human uniqueness. As the results from the trap-tube exemplify, failure of the great apes on a cognitive task does not mean that no other animal will succeed. We simply do not yet know if, for example, New Caledonian crows have diagnostic learning. It may seem unlikely that a species with a brain the size of a walnut may be capable of such cognition, but then in 1995, who would have predicted that members of the crow family would manufacture wooden hook tools or plan for the future?

This is not to say that we disagree with attempts to draw conclusions about what cognition is used by humans during tool use, or with the highlighting of how weak the single-factor argument for human uniqueness is. In contrast, summarizing the field to date and suggesting the potential boundaries between humans and other animals in the tool domain will drive and focus research effort on understudied areas, such as diagnostic learning and functional representation. Our cherry-picking mental time travel is simply to highlight that much may change in the future. Who knows where the boundaries will lie in 10 years time.

Cultural intelligence is key to explaining human tool use

doi:10.1017/S0140525X11001968

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Abstract: Contrary to Vaesen, we argue that a small number of key traits are sufficient to explain modern human tool use. Here we outline and defend the cultural intelligence (CI) hypothesis. In doing so, we critically re-examine the role of social transmission in explaining human tool use.

Vaesen presents a list of social and cognitive factors that he believes, in concert, explain the differences between human and chimpanzee tool use. We believe that Vaesen is too quick to reject explanations based on a smaller number of key traits; in particular, the traits outlined in the cultural intelligence hypothesis.

Cultural intelligence (CI) can come about in two (potentially complementary) ways. First, culture can enhance intelligence during an individual's lifetime ("ontogenetic" CI; Herrmann et al. 2007; Tomasello 1999). The ontogenetic CI hypothesis postulates that growing up in a culturally rich environment enables children to develop cognitive skills they would not otherwise have done (Moll & Tomasello 2007). According to this perspective, human-unique forms of social learning and teaching are responsible for qualitative changes in cognition – including changes in the ways in which we use tools. Therefore, at least some of the factors that Vaesen identifies as *causes* of human tool use are, in fact, *effects* of growing up in rich cultural environments.

Second, culture can play a role in the evolution of cognition across generations ("phylogenetic" CI; see also van Schaik & Pradhan 2003). Much less is known about this form of cultural intelligence. However, van Schaik & Pradhan (2003) modeled the co-evolution of culture and innovations and found that "high intelligence will often be a by-product of selection on abilities for socially biased learning." In other words, selection pressure for better social learning leads *indirectly* to the evolution of individual learning (and not vice versa).

In defense of his claims, Vaesen argues that as culture became more complex, greater intelligence was needed in order to deal with increasingly sophisticated cultural artifacts. However, this neglects the possibility that culture positively impacts on intelligence – as posed by the two CI hypotheses. In support of this perspective, Enquist et al. (2008) modeled cultural accumulation and showed that culture would level off unless faithful forms of social transmission impact on innovation levels. As culture has increased exponentially in modern humans, the most plausible view is that culture and intelligence form a feed-forward loop.

So far we have suggested that cumulative culture explains human intelligence in general, and sophisticated forms of tool use in particular. What then explains the existence of cumulative culture? We believe that the answer lies in species-unique forms of social learning and teaching.

Vaesen identifies a number of potential differences between social learning in humans and in chimpanzees. Although these differences may be accurate, we believe that the most basic differences between human and chimpanzee social learning lie elsewhere. Below we outline our alternate account of social learning in chimpanzees and compare it with the case of human children.

After critically reviewing the available evidence on social learning in chimpanzees, Tennie et al. (2009) argued that chimpanzee cultures are best described as serial reinventions across multiple generations. Social learning can still play some role in explaining the distribution of behaviors over time and space (e.g., Whiten et al. 1999), as it can increase the chance of reinvention. Social learning could even be responsible for cases in which the best target for a particular behavior is found and maintained over time (e.g., the whereabouts of the most bountiful feeding place). But the form that chimpanzee behaviors (including these "cultures") take is most strongly determined by biological and ecological factors. This account is supported by evidence suggesting that if chimpanzees copy behavioral forms (i.e., imitate) in the absence of training, then they do so rarely and/or not very precisely (Tennie et al. 2009; Whiten et al. 2009). In addition to this, teaching is virtually absent in chimpanzees (although see Boesch 1991). Without teaching, and with imitation severely limited, chimpanzees lack the transmission fidelity necessary to sustain true cumulative culture (where the form of behavior is transmitted). In turn, ontogenetic CI in chimpanzees (at least in the wild) is probably severely limited.

In contrast to social learning in chimpanzees, human social learning is typified by faithful transmission. Human children often imitate the specific actions of a model. Indeed, they do so even when it results in less efficient performance on their part (Nagell et al. 1993) and when they have been explicitly instructed not to (Lyons et al. 2007). This faithful transmission is at least partially the result of the social motivations and pressure underlying imitation (Over & Carpenter 2011). In contrast to chimpanzees, human children experience a strong drive to be like their group members (Nielsen 2009; Nielsen et al. 2008; Over & Carpenter 2009). This motivation can lead children to produce faithful copies of modeled acts even when it appears irrational to do so. Furthermore, humans often experience social pressure to imitate in particular ways. One form of social pressure is teaching. Gergely and Csibra (2006) have shown that even infants are sensitive to teaching cues and that they copy actions more

precisely when teaching cues are present. Social pressure to imitate can also come from the group in general. Haun and Tomasello (2011) have recently demonstrated that preschool children conform to the behavior of their peers and that they do so more in public than in private. Evidence from Rakoczy et al. (2008) suggests that not only do children experience social pressure; they exert it on those around them by enforcing social norms.

Thus, in contrast to Vaesen, we emphasize that a small number of key factors (e.g., imitation and teaching) render human culture a more social enterprise than is chimpanzee culture. Over time, these factors have played a causal role in producing qualitative changes in human cognition, including in the ways we use tools.

ACKNOWLEDGMENT
We thank Richard Moore for helpful comments.

Neurocognitive anthropology: What are the options?

doi:10.1017/S0140525X11002111

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Abstract: Investigation of the cerebral organization of cognition in modern humans may serve as a tool for a better understanding of the evolutionary origins of our unique cognitive abilities. This commentary suggests three approaches that may serve this purpose: (1) cross-task neural overlap, referred to by Vaesen; but also (2) co-lateralization of asymmetric cognitive functions and (3) cross-functional (effective) connectivity.

On several occasions in his systematic comparison, Vaesen refers to neuroscientific data to make his argument. In some instances, he underlines the absence of certain functional regions in the brains of non-human primates that are relevant for tool manipulation and production (Orban et al. 2006). In other sections the author points to the human recruitment of the same specialized cortical regions during different tasks of complex motor behavior such as speech or tool manipulation (Higuchi et al. 2009; Stout et al. 2008). The latter neuroscientific findings are taken as evidence for a common origin of tool use and language.

The use of neuroimaging and neurobehavioral research to speculate on evolutionary theories of cognition maybe tempting, but for the moment the available information is limited. I suggest that there are three major observations that can be employed in the discussion of neurocognitive evolution in humans: (1) neural overlap, (2) co-lateralization, and (3) cross-functional (effective) connectivity.

Cross-task neural overlap, or *neurofunctional overlap*, refers to the observation that a single brain region is recruited by different cognitive tasks. In neuropsychological studies, neurofunctional overlap is hinted at by the frequent co-occurrence of cognitive deficits, such as aphasia with apraxia or finger agnosia with acalculia; but lesion research provides only limited spatial resolution. Neuroimaging sparked a much more detailed investigation of the brain's functional organization, including clear cross-task activation in brain regions that can be measured at the 2–4 mm scale. Increased spatial resolution also allowed for a more detailed description of the match of cross-task neural overlap (*overlap correspondence*), although I'm unaware of systematic studies using this approach. The detection of overlapping neurocognitive circuits in specific cortical locations has been interpreted in terms of a functional and even evolutionary link, for example, between spatial and numerical processing (Hubbard et al. 2005; Walsh 2003) or between language and tool use (Arbib 2005; Higuchi et al. 2009).

The question remains whether overlapping neural responses reflect activation of the same or different neuronal populations. Separate neuronal populations may be interleaved in the same cortical area on a spatial scale below the resolution of conventional fMRI, in which case the corresponding neural circuits may function independently, yet show co-morbidity when this region gets damaged or disrupted. Despite this caveat, we may assume that the neural network activated by a given cognitive function is not randomly distributed over the cortex, but that it engages regions that are of strategic relevance for that function given its connections with other regions. Co-activation of the same region by different cognitive tasks therefore at least suggests a strategic similarity in the recruitment of a specific cortical area with its particular connections, that may or may not share neuronal resources. The shared neural localization of certain domain-general skills, such as hierarchical processing, also enticed scholars to theorize on the specificity and chronology of cognitive evolution (Arbib 2005). For the time being, these valuable hypotheses remain to be tested.

Co-lateralization is defined here as the covariance in the side and degree of hemispheric preference of two cognitive functions. Although many functions are asymmetrically represented in the brain, similarity in hemispheric preference as such is generally not considered to reflect a specific functional link, and there exists remarkably little research on the strength of lateralization within, let alone across, cognitively induced neural activation patterns (Pinel & Dehaene 2010). Significant correlations in the degree of asymmetric activation on sites of neural overlap would strengthen claims of biological association between cognitive functions.

A potentially very interesting source of information may be found in people with atypical language lateralization, such as in some extreme left-handers or in patients who suffered early brain damage. In these individuals it is possible to investigate how the atypical language dominance impacts on other lateralized cognitive abilities (Kroliczak et al. 2011). Recently, we compared a group of atypical language-dominant volunteers with a matched group showing typical language dominance on a tool-pantomiming paradigm while undergoing fMRI. In the group with atypical right language dominance, all individuals also demonstrated atypical right-hemispheric preference for praxis. Activation patterns for the language and praxis tasks revealed neural overlap in five cortical regions that showed highly correlated lateralization indices within and across tasks (Vingerhoets et al., in press).

So far, my arguments focus on the characteristics and interactions of the neural responses induced by different cognitive functions. Similarities in location and co-asymmetry should be supplemented by behavioral evidence of a link between cognitive traits. If two cognitive functions share an evolutionary origin, it is plausible to assume that they exhibit a functional bond over and above a common reliance on central resources such as attention and working memory. If, for example, tool use and linguistic tasks activate Broca's area (neural overlap) because they both require hierarchical structuring (underlying cognitive process), then we might expect behavioral interference between tool use and language tasks that manipulate hierarchical complexity.

Statistical dependencies in performance or neural activity only suggest a functional relation between cognitive traits or neural units, they do not entail causal information. Over the last years, several methods have been devised to investigate *effective (causal) brain connectivity* (Rubinov & Sporns 2010). In view of evolutionary queries, directional effects are of importance, as they may hint at the temporal order of cognitive evolvement. Similarities in the directional interactions of networks of related cognitive functions and causal effects of cross-task interference may help elucidate the chronological sequence of

neurocognitive evolution, such as the link between gestures and speech to explain the evolution of language.

I conclude that neuroscientific research on the cerebral organization of cognitive function in modern humans may contribute in unraveling the evolutionary trace of unique abilities such as tool use, language, and numerical cognition. Available methods for this endeavor include (1) detailed analysis of the neural overlap of activity patterns elicited by allied cognitive functions, (2) investigation of the correlation of co-lateralization in direction and degree across cognitive abilities that have an asymmetric hemispheric representation, and (3) comparison of the causal interactions in the neural networks of related cognitive functions and their cross-functional interference.

Motor planning in primates

doi:10.1017/S0140525X1100197X

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Abstract: Vaesen asks whether goal maintenance and planning ahead are critical for innovative tool use. We suggest that these aptitudes may have an evolutionary foundation in motor planning abilities that span all primate species. Anticipatory effects evidenced in the reaching behaviors of lemurs, tamarins, and rhesus monkeys similarly bear on the evolutionary origins of foresight as it pertains to tool use.

In discussing the impact of executive control on cumulative culture, Vaesen asks whether goal maintenance and planning are crucial for innovative acts – in particular, for innovative acts involving tool use. In this connection, we point to our work on goal maintenance and planning in two groups of nonhuman primates – cotton-top tamarin monkeys (Weiss & Wark 2009; Weiss et al. 2007) and lemurs (Chapman et al. 2010). The work we describe, as well as other research by us and others on anticipatory effects in reaching and grasping by humans (for reviews, see Rosenbaum 2010; Rosenbaum et al. 2006), may be unknown to Vaesen. Our aim in this commentary is to draw attention to this research, hoping that doing so will provide more tools with which Vaesen can evaluate and develop his hypothesis.

We have demonstrated that cotton-top tamarin monkeys (Fig. 1a) and lemurs (Fig. 1b) show a surprising level of goal maintenance and planning in a behavioral context. Our investigations reveal that these species spontaneously alter their object grasps depending on what they plan to do with the objects.

In these studies, the object to be moved was a cup with a piece of food stuck inside its bowl. The cup was positioned in a way that required manipulation of the cup to get the food out. The animals were allowed to interact with the cups as they pleased. Therefore, they could freely choose a canonical thumb-up initial posture followed by a non-canonical thumb-down posture, or they could freely choose a non-canonical thumb-down initial posture followed by a canonical thumb-up posture. These animals, like humans (Rosenbaum et al. 1990), chose the latter course of action. They adopted the non-canonical initial posture when grasping the cups to be inverted, thereby permitting the more canonical posture at the end of the cup rotation. The final thumb-up posture permitted greater control during the food extraction phase.

The pictures shown in Figure 1 are not rare instances of behavior, culled from video frames to finally find the poses we wanted. The pictures in Figure 1 illustrate behaviors that were reliably elicited whenever the cup needed to be turned to permit food extraction. When the cup did not need to be turned, the animals adopted canonical thumb-up postures right from the start. The statistics from the carefully controlled studies we did to test the hypothesis that the animals plan ahead supported this claim. On this basis, we concluded that the evolutionary foundation of human motor planning abilities as they relate to tool use are likely shared across all primate species. The latter inference is further supported by similar research with Old World monkeys (Nelson et al. 2010).

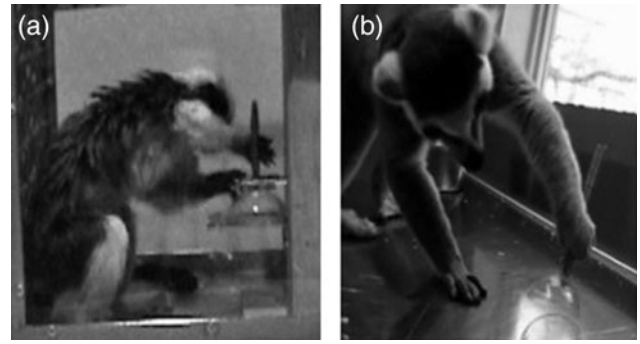

Figure 1 (Weiss). In (a), a cotton-top tamarin (*Saguinus oedipus)* grasps the stem of a cup (a plastic champagne glass with its base removed) to pull it from an apparatus and extract a marshamallow stuck in the cup's bottom. The tamarin uses a thumb-down grasp that permits a subsequent thumb-up grasp once the cup is pulled out and inverted (not shown). In (b), a ring-tailed lemur (*Lemur catta*) uses a thumb-down grasp to turn over a free-standing plastic champagne glass with a raisin affixed to the bottom of the bowl. Sources: (a) Weiss et al. 2007 (Courtesy of Sage Publications), (b) Chapman et al. 2010 (Courtesy of The American Psychological Association).

Vaesen is interested in behaviors that take longer to complete than the ones we have described here, so he could say we are focusing on too narrow a slice of behavior. Still, it has been argued that short-span motor abilities provide a scaffold for the evolution of planning and goal maintenance over longer durations. One proposal is that the cognitive capacities underlying anticipatory motor planning in reaching and grasping provide a sufficient condition for the development of tool use (Johnson-Frey 2004). We believe, contrary to Johnson-Frey, that such cognitive capacities provide a necessary but not sufficient condition for tool use. Our reason for this alternative view is that tamarins and lemurs do not use tools in the wild or in captivity, at least as far as we know, yet they show the anticipatory motor planning abilities needed to turn cups in ways that afford maximal control during food extraction. The underlying cognitive abilities indexed by our tasks require an appreciation of means-end relationships as well as an ability to inhibit the deployment of canonical postures in the service of better later postures. Our appreciation of these facts leaves us skeptical of Vaesen's claim that humans possess unique abilities for inhibition and foresight.

A last thought: In his discussion of foresight in the context of prospective planning of action sequences (sect. 12.2), Vaesen differentiates between novel solutions and action routines. We question whether that distinction properly distinguishes humans from non-human animals. The nonhuman primates in our studies found novel solutions for the food extraction problems they faced. They had minimal experience with cups, yet they spontaneously adopted non-canonical grasps when presented with inverted cups, even in first trials. If foresight requires novel solutions to problems, as Vaesen asserts, then the behaviors we have described provide evidence for prospective planning and foresight in non–tool-using animals.

Author's Response

From individual cognition to populational culture

doi:10.1017/S0140525X11002196

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Abstract: In my response to the commentaries from a collection of esteemed researchers, I reassess and eventually find largely intact my claim that human tool use evidences higher social and non-social cognitive ability. Nonetheless, I concede that my examination of individual-level cognitive traits does not offer a full explanation of cumulative culture yet. For that, one needs to incorporate them into population-dynamic models of cultural evolution. I briefly describe my current and future work on this.

Let me start with a somewhat obvious caveat. Given the overwhelming amount of feedback I received, my response will miss out on numerous topics worthy of further discussion. I regret not being able to fully honor the careful thought and work put into each commentary, and I sincerely hope my response does not distort matters too much.

Below I do four things. First, I defend my methodology against three points of critique (sect. R1). Second, I reassess the nine cognitive capacities of the target article in light of the open peer commentary (sects. R2–R8). I conclude that my original conclusion stands firm: Human tool use still reflects a profound discontinuity between us and chimps in matters of social and non-social wit. Third, I briefly take up a topic underplayed in the target article, namely, the evolutionary history of the cognitive traits reviewed (sect. R9). Fourth, I reconsider a topic I found underplayed in the commentaries, namely, the question of technological accumulation (sect. R10). I sketch how I am currently incorporating the cognitive assumptions made explicit in the target article into existing population-dynamic models of human cultural evolution; I sketch, thus, how I am making the necessary move from the individual level to the level where cumulative culture must be studied eventually, namely, that of the population.

R1. Methodological notes

R1.1 Why chimpanzees?

In the target article, I justified my narrow focus on humans and chimpanzees primarily on pragmatic grounds (see target article Note 1): For reasons of space, and given the wealth of data on primate tool use, I used chimps, rather than crows, finches, dolphins, otters, or elephants, as a contrast class for humans. Obviously, albeit implicitly, my justification also assumed some argument by ancestry (as **Cachel** observes). In the absence of direct evidence of ancestral states, our closest relatives may serve as, be it imperfect, models for reconstructing human cognitive and technological evolution (McGrew 1993). Finally, my focus on chimpanzees was justified by the second part of the paper, where I attempted to explain the vast discrepancy in technological accumulation between us and our closest relatives. The choice for the latter was not coincidental: Chimpanzees follow us on the technological accumulation list, so they offer a natural benchmark for examining which add-ons may account for the technological complexity observed in our lineage.

However, several commentators – most notably **Patterson & Mann**, **Reader & Hrotic**, and **Taylor & Clayton** – question my approach and stress the importance of including data on other (tool-using) animals. Such an extended comparative approach would allow me: (1) to see that none of the nine traits is *necessary* for tool use (Patterson & Mann); (2) to establish more realistic ancestral states (Reader & Hrotic); and (3) to determine the socioecological conditions under which tool use emerges (Patterson & Mann, Reader & Hrotic, Taylor & Clayton).

Although there is much to be said in favor of the two last points, let me first briefly dismiss point one. **Patterson & Mann** attribute to me the claim that I have identified a set of *necessary conditions for tool use*. As the title of the target article suggests, however, my actual concern was explaining *human* tool use (rather than tool use, full stop). Moreover, as stated in the abstract, my aim was to identify traits that *could help explain why technological accumulation evolved so markedly in humans, and so modestly in the great apes*. In sum, identifying necessary conditions for tool use was not one of the objectives of the target article.

Regarding the second point, **Reader & Hrotic** remark that contemporary chimpanzees likely misrepresent ancestral states. Differences between us and chimpanzees may be due to loss of traits in chimpanzees, rather than – as I assume – independent evolution of traits in us. Therefore, to decide which course evolution has taken (loss of the trait in chimps versus its acquisition by us) for any trait, the ancestral state must be established, which requires incorporating additional species. In this regard, Reader & Hrotic cite as a fruitful example a study by de Kort and Clayton (2006), who use phylogenetic analysis to reconstruct the ancestral state for caching behavior in corvids. de Kort & Clayton's methodology seems promising indeed. At this point, however, I have two worries. First, when it concerns a behavioral trait as cumulative culture, phylogenetic analyses will not be very helpful, given the apparent lack of the trait in other primate taxa – except perhaps in chimpanzees. Second, supposing one is interested in more basic traits (e.g., function representation, causal reasoning, theory of mind), phylogenetic analysis allows one to reconstruct ancestral states only on the condition that the trait in question has been properly diagnosed in all taxa under consideration. Reader & Hrotic's favored approach therefore still calls for carefully executed comparative work. The target article has done some of that necessary preparatory work, even if just for two species (i.e., humans and chimps).

Third, **Patterson & Mann**, **Reader & Hrotic**, and **Taylor & Clayton** correctly point out that the inclusion of other taxa may shed light on the socioecological conditions under which tool use emerges. For example, the fact that chimpanzees do not exhibit a certain trait may be due not so much to the absence of the trait as to its being unexpressed under current ecological conditions (for a similar point, see also **Nonaka**). Comparisons with

other taxa may prove valuable here – especially given the declining number of habitats occupied by wild chimpanzees. But unfortunately, inter-taxa comparisons will not suffice either. Much of what is said to be known about human cognition is based on studies of Westerners (see Note 44; see also Haun et al. 2006; Henrich et al. 2010). To rule out that their behavior was prompted by their specific ecological and/or cultural niche, many more cross-cultural studies have to be performed. In other words, in addition to inter-taxa comparisons, we also need *intra*-taxa comparisons, within our species in particular. Therefore I am even more skeptical than Taylor & Clayton are: I do not just believe that the conclusions of my paper may be premature, I am certain that they are. Still, they are as good as they can get given the present state of the field.

R1.2 Why not the environment?

Some commentators argue that the environment not just passively prompts certain behaviors, as just mentioned, but often plays a more active role. The environment, both natural and artificial, may scaffold cognition (**Jeffares** and **Blitzer & Huebner**). Instead of being localized exclusively in the head, cognition is an "intertwining of neural, bodily, and [external] material resources" (**Malafouris**). This kind of "ecological" approach to cognition is virtually absent in my story – much to the regret of Jeffares, Blitzer & Huebner, and Malafouris.

The reason for this omission has nothing to do with methodological prejudice, as I am very sympathetic to the movement set afoot by Andy Clark and others (see e.g., Clark et al., forthcoming). The omission is rather due to a lack of comparative evidence. To date, research on nonhuman species still works within an internalist mindset. Consequently, little to nothing is known about the scaffolds of the chimpanzee mind. Even our understanding of the importance of the external world in human cognitive processes is limited. Consider an example by **Jeffares**. He argues that the idea of a tool need not be internally represented, because existing tools can take over this role. The thought is that existing tools can be used as a template for the production of new ones; and this is presented as a clever strategy of using the environment to store ideas that we otherwise would need to store internally. However, before we accept that this form of scaffolding decreases rather than increases cognitive demands, Jeffares must show empirically that it does not depend on, for example: a capacity to conceptualize the existing tool as being for a particular purpose; a capacity for inferential reasoning to infer a production process from the tool's functional properties; or a capacity for analogical reasoning to appreciate that the principles governing the template also (should) govern the copy. Relying on behavioral templates (also discussed by Jeffares) seems a more elegant strategy; but this was covered in the target article's section on social learning.

R1.3 Why (only one sort of) neurology?

The claims of **Malafouris**, **Jeffares,** and **Blitzer & Huebner** raise another methodological issue. If the environment actively shapes cognition and, relatedly, brains are profoundly plastic, what should we make of the neurological evidence in the target article? Am I not assuming too much that cognitive traits are "hardwired" (Jeffares's word), each corresponding to a piece of "phylogenetically novel wetware" (Blitzer & Huebner's words)?

I think I am not. The target article points to only one (!) suggestion of a humanique cortical specialization for a trait (my discussion of Orban et al. 2006; Stout & Chaminade 2007). Apart from a suggestion of neural overlap between language and tool use in human BA44 (my discussion of Higuchi et al. 2009), everywhere else neurological evidence concerns the recruitment of large brain structures: (pre)frontal cortex, (pre)motor cortex, parietal cortex, parietotemporal cortex, (non)lateralized distributed networks. Evidently, I do not believe, and did not suggest, that these large chunks of brain evolved specifically for the cognitive task in question. Finding out how cognitive labor is preferentially distributed across the brain does not entail a commitment to nativism nor blank-slateism.

I agree, however, with **Vingerhoets**' methodological concerns. He remarks that I cover only one type of neuroscientific data used for speculating on the evolution of cognition, namely, data from cross-task neural overlap (in my discussion of Higuchi et al. 2009), thereby ignoring two alternatives, namely, co-lateralization and cross-functional connectivity analyses. His point is well taken that these may be or may become just as useful.

R2. Hand-eye coordination

In her commentary, **Dounskaia** conjectures that differences in human and nonhuman primate motor control may contribute substantially to the uniqueness of human tool use. She offers compelling evidence for the idea that some limb movements require much more cognitive effort than others do. The ability to perform accurately even these more effortful movements, Dounskaia suggests, may have enabled humans to deploy much more sophisticated tools.

At present, however, she lacks proper comparative evidence. Although it seems true that the repertoire of human motor actions greatly exceeds that of nonhuman primates, **Dounskaia** still needs to establish that this difference is attributable to a difference in the ability to perform more complex gestures. Chimpanzees may have such an ability but not, say, the creativity to exploit it. In this respect, Dounskaia's argument may benefit from an observation made in the target article. Chimpanzees have less neural tissue devoted to their locomotor muscles (Walker 2009), so that they must recruit larger numbers of motor units at once. This limits their ability for fine motor control, and arguably, the level of movement complexity they can achieve. Regardless, I certainly find Dounskaia's leading joint hypothesis promising enough to warrant further research, especially in a comparative setting.

Jacquet, Tessari, Binkofski, & Borghi (**Jacquet et al.**) argue that human tool use does not need to involve the high-level cognitive skills I discuss, as it may be based on much simpler detection systems. Their primary example is affordance perception: Humans are able to recognize manipulation opportunities, "matching the perceived physical features of objects and the agent's

biomechanical architecture, *goals, plans, values, beliefs, and past experiences*" (italics added). The text in italics not only shows that Jacquet et al. deviate substantially from J. J. Gibson's original formulation of affordances, it threatens to undermine their argument.

J. J. Gibson (1979) indeed introduced affordance perception as a fairly low-level process. Affordance perception referred to an animal's unreflective capacity to discern in the environment possibilities for action, only constrained by its own physical constitution (e.g., that a rake can be grasped; that it *affords* grasping). As such, affordance perception was a capacity also exhibited by animals that did not have *goals, plans, values*, or *beliefs*. Goals, plans, values and beliefs were added as constraints only in the work of Norman (1988), whose research primarily concerned humans. Norman's reformulation (which **Jacquet et al.** adopt) is not merely terminological. It implies a shift of focus from direct, low-level perception to indirect perception; that is, perception dependent on interpretation and background knowledge. With an example of Norman's, a knob on a refrigerator may be directly perceived as turnable (per Gibson), but one needs a Normanian conceptual model to perceive it as "to-lower-the-temperature-with–able." Likewise, the "Delete" key on a keyboard may be directly perceived as pressable (per Gibson), but one needs a Normanian conceptual model to perceive it as "to-delete-a-character-with–able."

In sum, **Jacquet et al.** face a dilemma. They either endorse a Normanian notion of affordance, thereby making affordance perception a conceptually rich, and fairly demanding, enterprise (as the target article's section on function representation suggested). Or they pursue a Gibsonian account, at the cost of being unable to explain the humanique ways in which humans navigate their humaniquely engineered environments.

R3. Body schema plasticity

Arbib and **Longo & Serino** find my conclusions regarding body schema plasticity uncompelling. According to these commentators, the question is not so much whether nonhuman primates *can* extend their body schema, but whether this happens as flexibly and rapidly as in humans. That question, Arbib and Longo & Serino believe, should be answered with a clear "no."

I remain unconvinced. Let me start with **Arbib**. Arbib refers to a study by Arbib et al. (2009) in support of his argument. Now, Arbib and colleagues observe the facility humans have in tool use, and infer from that fact that human body schema plasticity has unique properties (p. 458). But this does not follow. Tool use in nonhuman primates may be cumbersome due to numerous other reasons (limited grasp of causality, poor hand-eye coordination, and so forth). To be fair, this point is conceded a bit further in the text, when the authors suggest how *future* studies could establish the difference between humans and nonhuman primates as regards body schema plasticity. But in and of itself, the paper by Arbib et al. (2009) does not seem to provide the necessary evidence.

Longo & Serino's comparative evidence is wanting, too. They refer to a study by Quallo et al. (2009) in support of the idea that the body schema of monkeys is fairly rigid. Quallo and colleagues indeed demonstrate fairly persistent increases of gray matter in, among other places, the intraparietal sulcus of macaques that were trained to use a tool. Still, what Longo & Serino do not mention is that similar increases were observed in human volunteers learning to juggle (reported by Draganski & May 2008, as cited by Quallo et al. 2009).

R4. Causal reasoning

By and large, commentators propose three useful extensions to the target article's section on causal reasoning.

First, that the section would have benefited from discussions of experimental paradigms other than trap-tube tasks (**Taylor & Clayton**) and of experimental paradigms other than those presented in the target article's Figure 1 (**Cachel**). In light of the study by Seed et al. (2009), Taylor & Clayton remark, for example (as I do), that the reason for the modest performance of chimpanzees in trap-tube tasks may be demands posed by the tool aspect of the task; that is, that the extra cognitive load may block the animals' ability to properly assess the task's causal set-up. Other changes, such as allowing animals to push rather than pull the food item in the tube, may also yield different results (Mulcahy & Call 2006a). In sum, one should not draw too strong conclusions about great ape causal cognition from only one, potentially confounded test. Perhaps Taylor & Clayton are right that trap-tubes received too much attention in my paper. On the other hand, I do shortly describe three other of Povinelli's (2000) seminal experiments (see also Fig. 1): the flimsy-tool problem, the inverted-rake problem, and the table-trap problem. Chimpanzees performed poorly on these tests too; and, as Cachel is right to point out, Povinelli's book describes even more experiments, which together are at the very least suggestive of the fact that chimpanzees' grasp of causality is rather modest. There is little follow-up research based on these other paradigms, which is rather unfortunate indeed.

Second, **Penn, Holyoak, & Povinelli** (**Penn et al.**) miss a treatment of non-mechanism approaches to causal understanding. Indeed, in the target article I suggested that causal understanding requires the cognizer to infer a mechanism that relates the cause to the effect. This mechanism account is associated most prominently with Ahn and colleagues (Ahn & Kalish 2000; Ahn et al. 1995) and is fairly intellectualist:

> We suggest that people's beliefs about causal relations include (1) a notion of force or necessity, (2) a belief in a causal process that takes place between a cause and an effect, and (3) a set of more or less elaborated beliefs about the nature of that mechanism, described in theoretical terms. (Ahn & Kalish 2000, p. 302)

Penn et al. are right that there are other, less-demanding accounts of causal understanding. For example, Waldmann and Holyoak (1992; Waldmann et al. 1995) argue that human mental representations of cause-effect relations are organized into causal models. Basic causal models include representations of directionality (e.g., the causal arrow between A and B goes from A to B, not the reverse), strength (A impacts strongly/weakly on B), and polarity (A makes B happen versus A prevents B from happening); they typically do *not* refer to the mechanisms

responsible for the said cause-effect relation. A cognizer may know that there exists a strong causal arrow from eating rotten food to diarrhea without appreciating the unobservable underlying mechanisms – say, how bacterial toxins derange the normal bowel flora.

This position clearly conflicts with the view of Ahn & Kalish (2000; with their third point in the quote above in particular), but it can still be made to fit with the idea that chimpanzee causal understanding is limited. Using the terminology of **Penn et al.**, chimpanzees may be able to represent "first-order" causal models, but not "higher-order" ones. That is, whereas chimpanzees may be able to reason about the causal relationships between observable contingencies, they do not generalize these principles into higher-order "intuitive theories" (Penn et al. 2008), which typically refer to unobservable causal properties, such as gravity. Whereas for chimpanzees causal arrows between A and B remain on a perceptual level, no such limitations hold for the human case.

A third extension to my discussion of causal reasoning is offered by **Orban & Rizzolatti**, and it concerns a putative neuronal basis for the enhanced grasp of causality observed in humans. They refer to a study by Peeters et al. (2009), who found evidence that a specific sector of left inferior parietal lobule (i.e., anterior supramarginal gyrus, or aSMG) was activated in humans during the observation of tool use, but not in monkeys. Importantly, aSMG is not involved in understanding causal relationships in general; it codes tool actions in terms of the causal relationship between the intended use of the tool and the result obtained by using it. This study is interesting for at least two reasons. First, it may resolve some of the uncertainties regarding production-level representations of tool use skills (see Note 18). That is, aSMG may support larger motor repertoires, thereby supporting larger toolkits. Second, with the proviso that Peeters and colleagues studied rhesus monkeys and not chimpanzees, aSMG may perhaps explain why, as observed above, chimpanzees fail the trap-tube task when tools are implied. To wit, human aSMG would provide the computational power needed to overcome the additional demands posed by the tool aspect of the task.

R5. Function representation

Commentaries on the target article's section on function representation reveal some confusion as regards the notion of function. Several authors (i.e., **Blitzer & Huebner**; **Osvath, Persson, & Gärdenfors** [**Osvath et al.**]; **Patterson & Mann**; **Penn et al.**) argue that monkeys and apes are able to form functional representations, because these animals are capable of distinguishing between "functional" and "non-functional" tools (see e.g., Osvath & Osvath 2008) and are able to distinguish between "functionally" relevant (e.g., the shape of a rake) and "functionally" irrelevant (e.g., the color of the rake) properties of a tool (see e.g., Santos et al. 2003). Where these authors refer to functionality, I would speak rather of causal efficacy: An ape may appreciate that a certain rake is causally efficacious for food retrieval, but this does not mean it attributes to the rake that function. For that to happen, the ape must somehow conceive the rake as being for the said purpose. To get a feeling for the distinction: I may appreciate that a cup is causally efficacious to be used as a paperweight without attributing to it that particular function.

How could we know whether nonhuman primates form such permanent function representations? One way is to see whether they stick to a tool when functionally equivalent alternatives become available. The target article referred to a study by Cummins-Sebree and Fragaszy (2005) suggesting that they do not. **Patterson & Mann**, however, are right to point out that Whiten et al. (2005) may count as counter-evidence. In that study, chimpanzees continued to use a tool for its function even in the presence of functional equivalents.

Second, evidence of re-use of tools would support the idea of stable function attributions. I suggested that reports of tool re-use are scarce, with the exception of a study by Carvalho et al. (2009). Thanks to **Blitzer & Huebner**, I can here add a study by Sanz and Morgan (2010).

Finally, observations of functional fixedness would indicate that tools are conceptualized as being for one particular purpose rather than another. The target article suggested that functional fixedness was a humanique phenomenon. Yet, a study that was not available at the time of writing the paper – performed by Hanus et al. (2011) and pointed out to me by **Patterson & Mann** and **Rizzo –** may prove me wrong. Hanus and colleagues indeed provide suggestive evidence for functional fixedness in chimps. What remains to be seen, however, is whether chimpanzees' fixedness attests to a conceptual system storing functional information (as in humans), rather than being the result of associative learning, where repeated exposure to a tool's function blocks alternative, more creative uses.

For all three diagnostic features, it appears, commentators have raised quite forceful counter-arguments. Contrary to what I stated in the target article, it may therefore well be that nonhuman primates attach particular functions to particular objects. Whether they hereby rely on a conceptual system storing functional knowledge remains uncertain, as well as the question of what difference that would make.

Incidentally, **Gainotti** makes an intriguing remark about the conceptual system implied in human functional representation. He observes that tool concepts are typically represented unilaterally in a left-sided fronto-parietal network, because of their close link to actions, which are typically performed by the contra-lateral right hand. Living category concepts (e.g., about animals, plants), by contrast, rely more on visual data and are therefore stored in a bilateral network comprising rostral and ventral parts of the temporal lobes.

R6. Executive control

The target article subdivides executive control into mechanisms of monitoring online action, inhibition, foresight, and autocuing. Commentaries primarily take issue with my treatment of the latter two. **Weiss, Chapman, Wark, & Rosenbaum** (**Weiss et al.**) and **Osvath et al.** challenge my views concerning foresight; **Stoet & Snyder** add considerable refinement to my discussion of autocuing. Finally, the commentary by **Beck, Chappell,**

Apperly, & Cutting (**Beck et al.**) sheds new light on the role that executive control plays in tool innovation. Let me consider each commentary in turn.

Weiss et al. describe research evidencing anticipatory effects in the reaching behaviors of lemurs, tamarins, and rhesus monkeys. These monkeys were shown to prefer non-canonical hand postures in preparation of a subsequent grasping task. Such behavior, the authors point out, indicates some form of planning ahead. I agree. Still, the behavioral evidence does not meet the standards of foresight set in the target article; that is, it does not involve the formation of long-term goals, nor the prospection of needs other than those experienced in the immediate present. I certainly do not mean to downplay the significance of more basic forms of foresight, as those described by Weiss and colleagues. I believe indeed that these may increase our understanding of the evolution of planning and goal maintenance. To press the issue, however, the target article focused on those types of foresight where discrepancies between humans and nonhuman primates might be most apparent. In a search for discontinuities, I think, such an approach is justified. Nonetheless, I admit that to do right to the short-span motor-planning abilities discussed by Weiss et al., one would need to start with a much finer grained subdivision of executive control than the fourfold subdivision I deployed.

According to **Osvath et al.**, the target article misinterprets a study on great ape foresight by Osvath and Osvath (2008). They argue that I dismiss Osvath and Osvath's results too readily as a consequence of associative learning rather than as a consequence of foresight. In light of a paper by Osvath (2010) that Osvath et al. refer me to, I am willing to concede (again) that the experiments by Osvath and Osvath properly control for associative learning. Yet, my other observation still holds: The results of Osvath and Osvath (2008) may be due to inhibitory strength rather than to forethought – at least if we evaluate their experiments by the standards they set themselves:

> [T]o ensure that the self-control setting offers competition between *different desires*, the stimuli in the choice situation must represent different kinds of rewards. The immediate reward must be qualitatively distinct from the future one; otherwise the outcome of the choice would only be an expression of inhibitory strength and not of the ability to distinguish the future oriented drive from the present oriented one. (p. 664, italics added)

The rewards that Osvath and Osvath believe to be tapping "different desires" are a grape and half a liter of rosehip berry soup. **Osvath et al.** agree, and they justify Osvath and Osvath's assumption based on the idea that "eating and drinking are dissimilar activities, with different physiological outcomes.'" This may be a salient distinction when the comparison concerns, say, eating a grape and drinking water, but much less so when it concerns eating a grape and drinking rosehip berry soup. These latter activities have at least one target in common: a craving for fruity sugars. On this construal, subjects in the experiments of Osvath and Osvath may well have exercised inhibitory strength, but not have anticipated a drive different from the present one.

Stoet & Snyder refer to a set of recent and fascinating studies that demonstrate endogenous control – or as I called it, autocuing – in monkeys. These animals appear capable of letting internal representations act as cues for their behavior, rather than merely reacting on external stimuli. The reason why I believe autocuing to be relevant for tool use differs from that of Stoet & Snyder. My thought, which does not conflict with the observations of Stoet & Snyder, is that it allows deliberate practice, needed to achieve skill in complex tool use. Stoet & Snyder also see a link with skill complexity, but spell this out in terms of enhanced concentration in humans. Humans appear less flexible to switch rapidly between endogenously controlled task representations. That, in turn, supports concentration, a necessary component of long-lasting and complex tasks, such as developing skill in complex tool use. Together, Stoet & Snyder's and my proposal make plausible why humans, compared with other primates, seem to be capable of learning so much more intricate tasks-sets.

Lastly, the commentary of **Beck et al.** targets one of the outstanding questions formulated at the end of the target article. There (sect. 12.2.1) I observed that executive control appears critical for innovative tasks, such as solving Tower of London problems, and I asked whether the same would hold for other innovative acts, especially those involving tools. Beck et al. report on evidence that tentatively supports my suggestion. The authors tested human children on a tool innovation task based on Weir et al.'s (2002) wire-bending problem. Children up to 5 years old had great difficulties fashioning a straight piece of wire to make a hook for retrieving a bucket from a vertical tube. Given that the children displayed a proper causal understanding of the task, Beck et al. suggest that the children's poor performance was due to the immaturity of their executive system. It is unclear, however, how much executive control is really needed for solving the wire-bending problem. Prototypical tests of executive function involve multi-step actions (e.g., the Tower of London task, the Six Element Test), where a solution must be planned ahead and kept in mind during each step of the task. No such goal maintenance is implied, it seems, in the single-step wire-bending problem, where the ultimate solution of the task and its execution can run almost in parallel. Future research on the performance of dysexecutive patients on similar single-step and open-ended tasks could perhaps corroborate the hypothesis of Beck et al.

R7. Social learning, teaching, social intelligence

Surprisingly few commentators seem to disagree with my presentation of primate social skills (social learning, teaching, and social intelligence). **Osvath et al.** find my treatment of theory of mind too short – I agree, but referred the reader to the much more detailed discussions by Penn and Povinelli (2007b) and Call and Tomasello (2008). **Moerman** points to the enormous impact of new kinds of social organization on recent technological developments – I fully agree, and consider this topic more fully in section R10. Finally, **Tennie & Over** believe that I too quickly reject explanations based on a small number of social traits. In particular, they make the following two claims: (1) Humanique forms of social learning and teaching are sufficient to explain cumulative culture; and (2) cumulative culture positively impacts on cognition,

giving rise to many of the non-social cognitive skills discussed in the target article.

In the target article, I provided two arguments that undermine **Tennie & Over**'s first claim: the problem of the Acheulean, and the fact that non-social skills are part and parcel of sophisticated forms of social learning. This may not have convinced Tennie & Over. Therefore, let me provide an additional argument, which I draw, quite ironically, from a study referred to by Tennie & Over themselves, namely, Enquist et al. (2008).

Tennie & Over invoke that paper in support of their second claim. Indeed, Enquist and colleagues show that exponential cultural accumulation requires feed-forward loops between culture and creativity (or "intelligence," as Tennie & Over call it). Whereas genetically evolved creativity may produce accumulation at a constant rate, only culturally evolved creativity has the power to yield accelerating accumulation. But what Tennie & Over omit to mention is that, according to the very same models of Enquist and colleagues, the process of accumulation can get started *only once genetically evolved creativity has evolved*. Genetically evolved creativity, *not* cultural transmission, is the primary genetic bottleneck for cumulative culture:

> The evolution of cultural transmission is often considered the main genetic bottleneck for the origin of culture, because natural selection cannot favor cultural transmission without any culture to transmit. Our models suggest that an *increase in individual creativity may have been the first step toward human culture*, because in a population of creative individuals there may be enough non-genetic information to favor the evolution of cultural transmission. (Enquist et al. 2008, p. 46, italics added)

Put differently, for Enquist and colleagues, cultural transmission is insufficient for sustaining processes of cumulative culture – pace **Tennie & Over**. Incidentally, Enquist and colleagues black-box the cognitive skills that make up genetically evolved creativity. In the target article I discerned at least two contenders: a capacity for causal reasoning (sect. 12.1) and enhanced executive control (sect. 12.2; see also **Beck et al.**).

Let me turn to **Tennie & Over**'s second claim. Here the idea is that cultural environments are responsible for qualitative changes in cognitive skills. Tennie & Over write: "[A]t least some of the factors that Vaesen identifies as *causes* of human tool use are, in fact, *effects* of growing up in rich cultural environments." This may be right. To have bite, however, Tennie & Over need to specify which traits are implied. And evidently, they need to show for every single trait on the list that it is culturally acquired rather than innate. I am prepared to go for either option; but at present, especially in the face of a disheartening scarcity of cross-cultural data, I think it is more honest to admit that the science is not settled yet.

R8. Language

IJzerman & Foroni provide an argument that is structurally similar to the one of **Tennie & Over**. What social learning is for Tennie & Over, language is for IJzerman & Foroni. That is, IJzerman & Foroni argue that I underestimate the role of language in supersizing humans' cognitive toolkit, and that I thereby overestimate the cognitive discontinuity between chimps and humans.

In response, let me repeat what I did and did not do in the target article. I compared humans and chimps with respect to nine tool-related cognitive skills (including linguistic ability, for that matter), and I found that humans excelled in almost all of them. Thereby, I deliberately bracketed questions of implementation. Our excellence may be hardwired, culturally acquired (as **Tennie & Over** propose), a side effect of our linguistic ability (as **IJzerman & Foroni** propose), or a bit of all three (see also sections R1.2, R7, and R9). In my opinion, IJzerman & Foroni overestimate how much we know about the impact of language on our cognitive toolkit to be able to adjudicate among these four scenarios, but I do not want to press that point. Instead, let me formulate two further critical remarks.

First, to be able to make their argument, **IJzerman & Foroni** must rely on a comparative assessment of the sort that the target article gives. For example, IJzerman & Foroni believe that language supersizes human planning abilities and executive control (**Blitzer & Huebner**, by the way, make a similar observation in passing). Such a claim makes sense only if humans have superior planning ability and superior executive control to begin with – indeed, precisely what the target article attempted to show. More generally, one does not need to prove a trait's independence from linguistic ability to be able to judge whether humans have it and how good they are at it.

Second, there is something in **IJzerman & Foroni**'s charges that I cannot help but perceive as a plain inconsistency. The claim that language *supersizes* the human cognitive toolkit at the very least suggests a profound cognitive discontinuity between us and chimps; yet, IJzerman & Foroni charge *me* with overestimating the cognitive discontinuity between humans and chimps.

The second strand of comments concerning language comes from **Holloway**, **Arbib**, and **Barceló-Coblijn & Gomila**. These commentators point out, either implicitly or explicitly, that I have neglected the possibility that tool use and language co-evolved. And indeed, it is rather unfortunate that the target article examined only accounts according to which the evolution of tool use played a causal role in the subsequent evolution of language.

Holloway observes striking similarities between human language and toolmaking. He refers to his seminal paper "Culture: A Human Domain" (1969), where he described the similarities as follows:

> [A]lmost any model which describes a language process can also be used to describe tool-making. . . . Both activities are concatenated, both have rigid rules about serialization of unit activities (the grammar, the syntax), both are hierarchical systems of activity (as is any motor activity), and both produce arbitrary configurations which thence become part of the environment, either temporarily or permanently. (p. 401)

Holloway's co-evolutionary thesis appears a bit further on:

> Tool-making and language are concordant. Selection favored the cognitive structures dependent on brain organization and social structure which resulted in both language and toolmaking. (p. 404)

These early ideas clearly resonate in the more recent accounts of **Arbib** and **Barceló-Coblijn & Gomila**. According to Arbib, the evolution of complex forms of imitation underwrites the co-evolution of language and toolmaking. Complex imitation, here, involves increased

capacities for recognizing and imitating hierarchically structured processes, needed for assembling both words (in the case of language) and actions (in the case of toolmaking) into superordinate structures.

Also **Barceló-Coblijn & Gomila** are keen to point out the profound similarities between toolmaking and language. In knotting, in particular, they see a formal structure of similar complexity to a context-sensitive grammar. Tying knots in nets and basketry, for example, cannot be specified as an iterable sequence of steps at the service of a higher-level constructive plan, because "each single operation [e.g., tying one of the knots of the net] is conditional on the state of the rest of the fabric and the physical forces the knot is supposed to resist."

There is much to be said in favor of the accounts of **Holloway**, **Arbib**, and **Barceló-Coblijn & Gomila**. Still, I have one worry, which is not sufficiently stressed in the target article. Attempts at determining structural commonalities between language and toolmaking are easy prey for charges of arbitrariness. Take Barceló-Coblijn & Gomila's claim that context-sensitive procedures emerged very recently, only with the advent of knotting in *Homo sapiens*. Now, compare this with Holloway's (1969) interpretation of Acheulean toolmaking:

> Taking each motor event alone, no one action is complete; *each action depends on the prior one and requires a further one*, and each is dependent in another way on the original plan. In other words, at each point of the action except the last, the piece is not "satisfactory" in structure. Each unit action is meaningless by itself in the sense of the use of the tool; it is meaningful only in the context of the whole completed set of actions culminating in the final product. (p. 402, italics added)

As far as I can tell, **Holloway** here interprets Acheulean toolmaking as a context-sensitive procedure, in which each single blow is conditional on past and future blows. In the absence of a rigorous method for making similarity judgments, it is hard to decide whose interpretation is correct, Holloway's or that of **Barceló-Coblijn & Gomila**. Even an analysis of hierarchical complexity in stone toolmaking as detailed and systematic as that of Stout (2011, referred to by **Arbib**) contains a fair amount of arbitrariness (as Stout himself admits, p. 1057); attempts to mirror his approach onto (proto)language would only add more of it. Presumably, similarity will keep residing in the eye of the beholder.

R9. Evolutionary issues

Even if one accepts my description of human tool-related cognitive abilities, how did all these abilities evolve? I am glad that so many commentators took up that pertinent question in my stead. Broadly speaking, their hypotheses fall into three groups.

First, **Crabb** endorses the view that human technological ingenuity emerged in response to a process of technological selection. He argues that hominids, unlike other tool-using species, depended on tools for their survival. The increasingly dry and open landscapes made our ancestors extremely vulnerable to attacks by predators; the use of weapons for protection would clearly confer fitness advantage. Subsequent elaborations on these early tools would have provided even more survival benefits, and as such, favor even more cognitive sophistication.

Crabb's hypothesis is reminiscent of, but interestingly different from, earlier technological intelligence hypotheses (for an elegant discussion, see Byrne 1997). According to these, tool use skills are favored whenever there is a premium on gains in efficiency with respect to (extractive) foraging; on Crabb's account, in contrast, the premium would initially be on gains in efficiency with respect to protection. What puzzles me, however, is how Crabb's account would accommodate the fact that the earliest known tools (i.e., Oldowan flakes) offer little protection against animal attacks. In this respect, earlier versions of the technological intelligence hypothesis seem to fare much better.

Second, several commentaries endorse some kind of cultural intelligence hypothesis. **Tennie & Over**, as discussed earlier, argue that the evolution of humanique forms of social learning and teaching subsequently drove the cultural evolution of other tool-related cognitive skills. **Nielsen** expresses a similar view, but adds quite a forceful argument in its favor. He observes that humans are the only species to have a childhood as a life stage, which provides ample opportunities for the acquisition of complex skills – including cognitive skills related to tool use. Finally, the examples of niche construction given by **Blitzer & Huebner**, **Jeffares**, **Nonaka**, and **Arbib** seem consistent with a cultural intelligence hypothesis, although not necessarily of the ontogenetic kind (as the one of Tennie & Over).

Third, there is the view that technical and sociocultural cognitive traits co-evolved, in concert with increasing brain size and reflecting a *general* cognitive ability. On this account – endorsed by **Reader & Hrotic**, **Gibson**, and perhaps **Penn et al.** – neither social nor ecological challenges alone account for human cognitive and brain evolution. In support of this view, Reader & Hrotic point to a very recent study by Reader et al. (2011), which I find particularly compelling. Reader and colleagues compiled cognitive measures from multiple domains (social, technical, ecological), examined their interrelations (for 62 primate species), and found strong cross-species associations. Rather than that each trait evolved in response to species-specific social and ecological demands, it therefore seems more likely that social, technical, and ecological traits evolved in concert, as part of a highly correlated cognitive suite.

R10. From individual cognition to population-level culture

My primary reason for examining primate social and nonsocial wit was the belief that doing so would help us to explain why technological accumulation evolved so markedly in us, and so modestly in chimps. To be sure, I was fully aware that an examination of cognitive capabilities alone would offer only half an explanation; that for the other part, one would need to study how these abilities play out at the aggregate level.

Therefore, I am in agreement with **Ragir & Brooks** that human cultural evolution cannot be properly understood if population and group dynamics are ignored. But the reverse holds as well: One needs accurate microlevel data to be able to give meaningful descriptions at the macro level. Consider, for example, Ragir & Brooks' contention that "changes in population density result in

the specialization of labor and knowledge," and that "as communities increase in size, functional institutions appear." Without a proper micro-level foundation, these explanations are highly unsatisfactory. Increasing population densities will favor specialization and functional institutions only in animals that meet certain cognitive requirements; otherwise, the animal kingdom would have been replete with species as cooperative and institutionalized as humans are.

Moerman appreciates this complementarity well. He finds my characterization of human tool-related cognitive abilities exemplary but insufficient to account for such astonishing achievements as cathedrals, iPhones, and symphony orchestras. To explain these, Moerman argues, one also needs to consider the novel ways in which humans tend to organize themselves, acting collectively towards otherwise impossible outcomes. Although the target article described a set of micro-level mechanisms that enable these forms of cooperation (see e.g., sect. 12.3.1 and 12.3.2), I agree that their impact remained somewhat elusive.

Therefore, as a natural follow-up, I already started developing an agent-based model to assess the impact of collective learning on cumulative culture. Preliminary results indicate that at certain levels of technological complexity, default mechanisms of individual and social learning are unable to sustain further accumulation; and that at that point, only collective learning is able to reboot the cumulative process. The model is also used to examine the effects of certain population characteristics; for example, how isolation and interconnectedness of subpopulations play out at higher levels of aggregation.

In the present version of the model, complexity is defined just in terms of the number of components that a technology has. In a later stage, however, complexity will also be a measure of the number of interactions between components. Based on a paper by Rivkin (2000), the prediction now is that, even given collective learning, cumulation levels off at a critical level of complexity; and that the process can recover once the causal relationships between components are understood. Thereby, the macro-level impact of another favored micro-level trait, namely, causal reasoning, would have been addressed.

R11. Conclusion

Despite a set of methodological worries and worries about the details of my argument, the target article's main contention, namely, that human tool use reflects higher cognitive ability, holds up pretty well. Only with respect to function representation may have my conclusions perhaps been too strong.

Evidently, there are plenty of topics worthy of further investigation, to begin with the outstanding questions formulated in section 12. Also, new experimental paradigms will undoubtedly force us to reformulate or refine our judgments about what humans and chimps can and cannot do. Furthermore, the methodological and evolutionary issues pointed out by the commentators are in need of clarification; and at various places I have said that I would welcome more comparative evidence. Finally, there is the question of how individual-level cognitive processes scale up to population-level phenomena. As suggested above, that question will concern me most in the time to come. But whatever the results of that future work, I hope my current efforts have already contributed, even a little, to our understanding of our humanique selves.

References

[The letters "a" and "r" before author's initials stand for target article and response references, respectively]

Acerbi, A., Tennie, C. & Nunn, C. (2011) Modeling imitation and emulation in constrained search space. *Learning & Behavior* 39(2):104–14. [POJ]

Adovasio, J. M., Sofer, O. & Klima, B. (1996) Upper Paleolithic fibre technology: Interlaced woven finds from Pavlov I, Czech Republic, c. 26,000 years ago. *Antiquity* 70:526–34. [LB-C]

Ahn, W. & Kalish, C. (2000) The role of mechanism beliefs in causal reasoning. In: *Cognition and explanation*, ed. R. Wilson & F. Keil, pp. 199–226. MIT Press. [arKV]

Ahn, W., Kalish, C., Medin, D. & Gelman, S. (1995) The role of covariation versus mechanism information in causal attribution. *Cognition* 54:299–352. [DCP, arKV]

Aiello, L. C. & Key, C. (2002) Energetic consequences of being a *Homo erectus* female. *American Journal of Human Biology* 14:551–65. [SR]

Aiello, L. C. & Wells, J. C. (2002) Energetics and the evolution of the genus *Homo*. *Annual Review of Anthropology* 31:323–38. [SR]

Andrews, G., Halford, G. S., Bunch, K. M., Bowden, D. & Jones, T. (2003) Theory of mind and relational complexity. *Child Development* 74(5):1476–99. [DCP]

Arbib, M. A. (2005) From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences* 28:105–24. [MAA, LB-C, aKV, GV]

Arbib, M. A. (2011) From mirror neurons to complex imitation in the evolution of language and tool use. *Annual Review of Anthropology* 40:257–73. [MAA]

Arbib, M. A. (2012) *How the brain got language: The mirror system hypothesis*. Oxford University Press. [MAA]

Arbib, M. A., Bonaiuto, J., Jacobs, S. & Frey, S. H. (2009) Tool use and the distalization of the end-effector. *Psychological Research* 73(4):441–62. doi: 10.1007/s00426-009-0242-2 [MAA, rKV]

Arbib, M. A. & Lee, J. (2008) Describing visual scenes: Towards a neurolinguistics based on construction grammar. *Brain Research* 1225:146–62. [MAA]

Asfaw, B., White, T., Lovejoy, O., Latemer, B., Simpson, S. & Suwa, G. (1999) *Australopithecus garhi*: A new species of early hominid from Ethiopia. *Science* 284:629–35. [TN]

Aunger, R. (2010) What's special about human technology? *Cambridge Journal of Economics* 34(1):115–23. [aKV]

Axelrod, R. & Hamilton, W. (1981) The evolution of cooperation. *Science* 211:1390–96. [aKV]

Banzi, M. (2008) *Getting started with Arduino*. O'Reilly/Make Books. [AR]

Barceló-Coblijn, L. (in press) Evolutionary scenarios for the emergence of recursion. *Theoria et Historia Scientiarum: International Journal for Interdisciplinary Studies*. [LB-C]

Barceló-Coblijn, L. (2011) A biolinguistic approach to the vocalizations of H. neanderthalensis and the genus Homo. *Biolinguistics* 5(4):286–334. [LB-C]

Barrett, L. (2011) *Beyond the brain: How the body and the environment shape cognition*. Princeton University Press. [AB]

Barsalou, L. W. (2005) Continuity of the conceptual system across species. *Trends in Cognitive Sciences* 9:309–11. [HIJ]

Barsalou, L. W. (2008) Grounded cognition. *Annual Review of Psychology* 59:617–45. [GG]

Bar-Yosef, O. (2002) The Upper Paleolithic revolution. *Annual Review of Anthropology* 31:363–93. [aKV]

Bassolino, M., Serino, A., Ubaldi, S. & Làdavas, E. (2010) Everyday use of the computer mouse extends peripersonal space representation. *Neuropsychologia* 48:803–11. [MRL]

Bavelier, D., Green, S. & Dye, M. W. (2010) Children, wired: For better and for worse. *Neuron* 9:692–701. [SR]

Beck, S. R., Apperly, I. A., Chappell, J., Guthrie, C. & Cutting, N. (2011) Making tools isn't child's play. *Cognition* 119:301–306. [SRB, MN]

Beer, R. D. (2000) Dynamical approaches to cognitive science. *Trends in Cognitive Sciences* 4(3):91–99. [AB]

Bentley-Condit, V. K. & Smith, E. O. (2009) Animal tool use: Current definitions and an updated comprehensive catalog. *Behaviour* 147(2):185–221. [EMP]

Bergson, H. (1911/1998) *Creative Evolution* (A. Mitchell, Trans.). Dover Publications. [LM, MN]

Bermudez, J. (2003) *Thinking without words*. Oxford University Press. [HIJ]

Berti, A. & Frassinetti, F. (2000) When far becomes near: Remapping of space by tool use. *Journal Cognitive Neuroscience* 12(3):415–20. [aKV]

Bickerton, D. (2009) *Adam's tongue: How humans made language, how language made humans*. Hill and Wang/Farrar, Straus and Giroux. [KRG]

Bird, C. D. & Emery, N. J. (2009) Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences* 106:10370–75. [SRB]

Biro, D. & Matsuzawa, T. (1999) Numerical ordering in a chimpanzee (*Pan troglodytes*): Planning, executing, and monitoring. *Journal of Comparative Psychology* 113(2):178–85. [EMP]

Biro, D., Sousa, C. & Matsuzawa, T. (2006) Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding. In: *Cognitive development in chimpanzees*, ed. T. Matsuzawa, M. Tomonaga & M. Tanaka, pp. 476–508. Springer. [aKV]

Blaisdell, A. P., Sawa, K., Leising, K. J. & Waldmann, M. R. (2006) Causal reasoning in rats. *Science* 311(5763):1020–22. [EMP]

Boesch, C. (1991) Teaching among wild chimpanzees. *Animal Behaviour* 41(3):530–32. [CT, aKV]

Boesch, C. (1994) Cooperative hunting in wild chimpanzees. *Animal Behaviour* 48:653–67. [EMP, aKV]

Boesch, C. (2002) Cooperative hunting roles among Taï chimpanzees. *Human Nature* 13:27–46. [aKV]

Boesch, C. & Boesch, H. (1984) Mental map in wild chimpanzees: An analysis of hammer transports for nut cracking. *Primates* 25:160–70. [aKV]

Boesch, C. & Boesch, H. (1989) Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology* 78:547–73. [EMP, aKV]

Boesch, C. & Boesch-Achermann, H. (2000) *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford University Press. [AB]

Boesch, C., Head, J. & Robbins, M. (2009) Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution* 56:560–69. [AB, aKV]

Bogin, B. (1990) The evolution of human childhood. *Bioscience* 40:16–25. [MN]

Boserup, E. (1981) *Population and technological change: A study of long-term trends*. University of Chicago Press. [SR]

Botvinick, M. & Cohen, J. (1998) Rubber hands 'feel' touch that eyes see. *Nature* 391:756. [MRL]

Boyd, R. & Richerson, P. (1985) *Culture and the evolutionary process*. University of Chicago Press. [aKV]

Boyd, R. & Richerson, P. (1995) Why does culture increase adaptability? *Ethology and Sociobiology* 16:125–43. [aKV]

Boyd, R. & Richerson, P. (1996) Why culture is common but cultural evolution is rare. *Proceedings of the British Academy* 88:73–93. [aKV]

Boysen, S. T. & Berntson, G. G. (1995) Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes* 21(1):82–86. [AB]

Bradshaw, J. & Nettleton, N. (1982) Language lateralization to the dominant hemisphere: Tool use, gesture and language in hominid evolution. *Current Psychological Reviews* 2:171–92. [aKV]

Bril, B., Rein, R., Nonaka, T., Wenban-Smith, F. & Dietrich, G. (2010) The role of expertise in tool use: Skill differences in functional action adaptation to task constraints. *Journal of Experimental Psychology: Human Perception and Performance* 36(4):825–39. [TN]

Brockmann, H. J. (1985) Tool use in digger wasps (Hymenoptera: Sphecinae). *Psyche* 92(2–3):309–29. [EMP]

Brosnan, S. & Beran, M. (2009) Trading behavior between conspecifics in chimpanzees, Pan troglodytes. *Journal of Comparative Psychology* 123:181–94. [aKV]

Brosnan, S. & de Waal, F. (2002) A proximate perspective on reciprocal altruism. *Human Nature* 13:129–52. [aKV]

Brosnan, S., Silk, J., Henrich, J., Mareno, M., Lambeth, S. & Schapiro, S. (2009) Chimpanzees (Pan troglodytes) do not develop contingent reciprocity in an experimental task. *Animal Cognition* 12:587–97. [aKV]

Bshary, R. & Grutter, A. S. (2005) Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters* 1:396–99. [SMR]

Bshary, R. & Grutter, A. S. (2006) Image scoring and cooperation in a cleaner fish mutualism. *Nature* 441:975–78. [SMR]

Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K. & Heinrich, B. (2007) Ravens judge competitors through experience with play caching. *Current Biology* 17:1804–808. [AHT]

Butler, S. (1912/1951) Tools. In: *Samuel Butler's notebooks*, ed. G. Keynes & B. Hill, pp. 115–24. Jonathan Cape. [AR]

Buxbaum, L. J., Sirigu, A., Schwartz, M. F. & Klatzky, R. (2003) Cognitive representations of hand posture in ideomotor apraxia. *Neuropsychologia* 41(8):1091–13. [aKV]

Byrne, R. (1997) The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence. In: *Machiavellian intelligence II*, ed. A. Whiten & R. Byrne, pp. 289–311. Cambridge University Press. [SMR, rKV]

Byrne, R. (2004) The manual skills and cognition that lie behind hominid tool use. In: *Evolutionary origins of great ape intelligence*, ed. A. Russon & D. R. Begun, pp. 31–44. Cambridge University Press. [aKV]

Byrne, R. W. & Whiten, A. (1988) *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Clarendon Press. [EMP]

Cachel, S. (2009) Natural history intelligence and hominid tool behavior. In: *Tools of the trade. Methods, techniques, and innovative approaches in archaeology*, ed. J. Wilkins & K. Anderson, pp. 13–29. University of Calgary Press. [SC]

Cachel, S. & Harris, J. W. (1995) Ranging patterns, land-use and subsistence in *Homo erectus* from the perspective of evolutionary ecology. In: *Human evolution in its ecological context. Palaeo-anthropology: Evolution and ecology of* Homo erectus, ed. J. R. Bower & S. Sartono, pp. 52–65. Leiden University. [SR]

Caldwell, C. & Millen, A. (2008) Social learning mechanisms and cumulative cultural evolution. *Psychological Science* 20:1478–84. [aKV]

Call, J. (2010) Trapping the minds of apes: Causal knowledge and inferential reasoning about object-object interactions. In: *The mind of the chimpanzee: Ecological and experimental perspectives*, ed. E. V. Lonsdorf, S. R. Ross, T. Matsuzawa & J. Goodall, pp. 75–86. University of Chicago Press. [EMP]

Call, J. & Tomasello, M. (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Science* 20:1478–84. [MO, AHT, arKV]

Calvin, W. (1990) *The ascent of mind*. Bantam. [aKV]

Calvin, W. (1993) The unitary hypothesis: A common neural circuitry for novel manipulations, language, plan-ahead, and throwing? In: *Tools, language, and cognition in human evolution*, ed. K. Gibson & T. Ingold, pp. 230–50. Cambridge University Press. [LB-C, aKV]

Camps, M. & Uriagereka, J. (2006) The Gordian knot of linguistic fossils. In: *The biolinguistic turn. Issues on language and biology*, ed. J. Rosselló & J. Martín, pp. 34–65. Publications of the University of Barcelona. [LB-C]

Carruthers, P. (2002) The cognitive functions of language. *Behavioral and Brain Sciences* 25(6):657–726. [AB]

Carruthers, P. (2005) The case for massively modular models of mind. In: *Contemporary debates in cognitive science*, ed. R. Stainton, pp. 205–25. Blackwell. [DCP]

Carruthers, P. & Smith, P. K. eds. (1996) *Theories of theory of mind*. Cambridge University Press. [DCP]

Carvalho, S., Biro, D., McGrew, W. & Matsuzawa, T. (2009) Tool-composite reuse in wild chimpanzees (Pan troglodytes): Archaeologically invisible steps in the technological evolution of early hominins? *Animal Cognition* 12:S103–14. [EMP, arKV]

Case, R. (1985) *Intellectual development: Birth to adulthood*. Developmental Psychology Series. Academic Press. [KRG]

Caselli, L. & Chelazzi, L. (2011) Does the macaque monkey provide a good model for studying human executive control? A comparative behavioral study of task switching. *PloS ONE* 6(6):1–9. [GS]

Casler, K. & Kelemen, D. (2005) Young children's rapid learning about artifacts. *Developmental Science* 8(6):472–80. [aKV]

Chambon, V., Domenech, P., Pacherie, E., Koechlin, E., Baraduc, P. & Farrer, C. (2011) What are they up to? The role of sensory evidence and prior knowledge in action understanding. *PloS ONE* 6(2):e17133. Retrieved from www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0017133. [POJ]

Chapman, K. M., Weiss, D. J. & Rosenbaum, D. A. (2010) Evolutionary roots of motor planning: The end-state comfort effect in lemurs (*Lemur catta, Eulemur mongoz, Eulemur coronatus, Eulemur collaris, Hapalemur griseus*, and *Varecia rubra*). *Journal of Comparative Psychology* 124:229–32. [DJW]

Cheney, D. & Seyfarth, R. (1990) *How monkeys see the world*. University of Chicago Press. [aKV]

Cheney, D. & Seyfarth, R. (1995) The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: Evidence for causal reasoning? *Journal of Comparative Psychology* 109(2):134–41. [EMP]

Cheng, P. W. (1993) Separating causal laws from casual facts: Pressing the limits of statistical relevance. In: *The psychology of learning and motivation, vol. 30*, ed. D. L. Medin, pp. 215–64. Academic Press. [DCP]

Cheng, P. W. (1997) From covariation to causation: A causal power theory. *Psychological Review* 104:367–405. [DCP]

Cho, S., Moody, T. D., Fernandino, L., Mumford, J. A., Poldrack, R. A., Cannon, T. D., Knowlton, B. J. & Holyoak, K. J. (2010) Common and dissociable prefrontal loci associated with component mechanisms of analogical reasoning. *Cerebral Cortex* 20:524–33. [DCP]

Chomsky, N. (1959) On certain formal properties of grammars. *Information and Control* 2:137–67. [LB-C]
Claidière, N. & Sperber, D. (2010) Imitation explains the propagation, not the stability of animal culture. *Proceedings of the Royal Society B: Biological Sciences* 277(1681):651–59. [POJ]
Clark, A. (1997) *Being there: Putting brain, body, and world together again.* MIT Press. [POJ]
Clark, A. (1998a) Twisted tales: Causal complexity and cognitive scientific explanation. *Minds and Machines* 8:79–99. Reprinted in *Explanation and cognition*, ed. F. Keil & R. A. Wilson. MIT Press 2000. [HIJ]
Clark, A. (1998b) Magic words: How language augments human computation. In *Language and thought: Interdisciplinary themes*, ed. P. Carruthers & J. Boucher. Cambridge University Press. [HIJ]
Clark, A. (2006) Language, embodiment, and the cognitive niche. *Trends in Cognitive Sciences* 10(8):370–74. [AB]
Clark, A. (2008) *Supersizing the mind: Embodiment, action, and cognitive extension*. Oxford University Press. [AB, HIJ, BJ, LM]
Clark, A. & Chalmers, D. (1998) The extended mind. *Analysis* 58:7–19. [BJ]
Clark, A., Pritchard, D. & Vaesen, K. (forthcoming) Introduction to special issue on "Extended cognition and epistemiology." *Philosophical Explorations*. 15(2) [rKV]
Clark, A. E. & Semin, G. R. (2007) Receivers' expectations for abstract versus concrete construal: Conversational relevance as determinant of construal level. *Journal of Language and Social Psychology* 27:155–67. [HIJ]
Clayton, N. S. & Dickinson, A. (1998) Episodic-like memory during cache recovery by scrub jays. *Nature* 395:272–78. [AHT]
Cole, M. (1996) *Cultural psychology*. Harvard University Press. [AR]
Collias, N. E. (1997) The origin and evolution of nest building by passerine birds. *Condor* 99:253–69. [MAA]
Connor, R. C. (2007) Dolphin social intelligence: Complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362(1480):587–602. [EMP]
Coolidge, F. & Wynn, T. (2005) Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeological Journal* 15:5–26. [aKV]
Corballis, M. (2010) Mirror neurons and the evolution of language. *Brain & Language* 112:25–35. [aKV]
Crabb, P. B. (2000) The material culture of homicidal fantasies. *Aggressive Behavior* 26:225–34. [PBC]
Crabb, P. B. (2005) The material culture of suicidal fantasies. *Journal of Psychology* 139:211–20. [PBC]
Crabb, P. B. & Elizaga, A. (2008) The adaptive value of tool-aided defense against wild animal attacks. *Aggressive Behavior* 34:633–38. [PBC]
Croft, W. (2001) *Radical construction grammar: Syntactic theory in typological perspective*. Oxford University Press. [MAA]
Csibra, G. & Gergely, G. (2006) Social learning and social cognition: The case for pedagogy. In: *Processes of change in brain and cognitive development, vol. 21: Attention and performance*, ed. M. Johnson & Y. Munakata, pp. 249–74. Oxford University Press. [aKV]
Csibra, G. & Gergely, G. (2007) "Obsessed with goals": Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica* 124:6078. [POJ, aKV]
Csibra, G. & Gergely, G. (2009) Natural pedagogy. *Trends in Cognitive Sciences* 13(4):148–53. [aKV]
Cummins-Sebree, S. E. & Fragaszy, D. M. (2005) Choosing and using tools: Capuchins (Cebus apella) use a different metric than tamarins (Saguinus oedipus). *Journal of Comparative Psychology* 119(2):210–19. [EMP, arKV]
Cutting, N., Apperly, I. A., Beck, S. R. (2011) Why do children lack the mental flexibility to innovate tools? *Journal of Experimental Child Psychology* 109:497–511. [SRB]
Cutting, N., Beck, S. R. & Apperly, I. A. (under review) Is there a complexity hierarchy in human children's tool making? [SRB]
Dally, J. M., Emery, N. J. & Clayton, N. S. (2010) Avian theory of mind and counter espionage by food-caching western scrub-jays (*Aphelocoma californica*). *European Journal of Developmental Psychology* 7(1):17–37. [EMP]
Darwin, C. (1871) *The descent of man, and selection in relation to sex*. John Murray. [PBC, LM]
Darwin, C. R. (1859) *The origin of species*. John Murray. [TN]
Davidson, I. & McGrew, W. C. (2005) Stone tools and the uniqueness of human culture. *Journal of the Royal Anthropological Institute* 11:793–817. [LM]
de Kort, S. & Clayton, N. (2006) An evolutionary perspective on caching by corvids. *Proceedings of the Royal Society B: Biological Sciences* 4:149–96. [SMR, rKV]
De Preester, H. & Tsakiris, M. (2009) Body-extension versus body-incorporation: Is there a need for a body-model? *Phenomenology and the Cognitive Sciences* 8:307–19. [MRL]
de Waal, F. (1989) Food-sharing and reciprocal obligations in chimpanzees. *Journal of Human Evolutionary Anthropology* 18:433–59. [aKV]
de Waal, F. (2000) Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour* 60:253–61. [aKV]
de Waal, F. (2006) *Primates and philosophers.* Princeton University Press. [aKV]
de Waal, F. B. M. & Ferrari, P. F. (2010) Towards a bottom-up perspective on animal and human cognition. *Trends in Cognitive Sciences* 14(5):201–207. [EMP]
Dean, M. C. (2000) Progress in understanding hominoid dental development. *Journal of Anatomy* 197:77–101. [MN]
Dean, M. C., Leakey, M. G., Reid, D., Schrenk, F., Schwartz, G. T., Stringer, C. & Walker, A. (2001) Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature* 414:628–31. [MN]
Deaner, R. O., van Schaik, C. & Johnson, V. (2006) Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology* 4:149–96. [SMR]
Defeyter, M. A. & German, T. P. (2003) Acquiring an understanding of design: Evidence from children's insight problem solving. *Cognition* 89(2):133–55. [aKV]
Dehaene, S., Spelke, E., Pinel P., Stanescu R. & Tviskin, S. (1999) Sources of mathematical thinking: Behavioral and brain imaging evidence. *Science* 284:970–74. [HIJ]
Delanges, A. & Roche, H. (2005) Late Pliocene hominid knapping skills: The case of Lokalalei 2C, West Turkana, Kenya. *Journal of Human Evolution* 48:435–72. [TN]
Dennett, D. C. (1982) Beyond beliefs. In: *Thought and object: Essays on intentionality*, ed. A. Woodfield, pp. 1–97. Oxford University Press. [POJ]
Dennett, D. C. (1995) *Darwin's dangerous idea.* Simon and Schuster. [POJ]
Dodgson, M. (1993) Organizational learning: A review of some literatures. *Organization Studies* 14:375–94. [aKV]
Donald, M. (1993) Human cognitive evolution. What we were, what we are becoming. *Social Research* 60:143–70. [GS, aKV]
Donald, M. (1999) Preconditions for the evolution of protolanguage. In: *The descent of mind: Psychological perspectives on hominid evolution*, ed. M. C. Corballis & S. E. G. Lea, pp. 355–65. Oxford University Press. [aKV]
Donald, M. W. (1991) *Origins of the modern mind: Three stages in the evolution of culture and cognition.* Harvard University Press. [SR]
Douglas-Hamilton, I., Bhalla, S., Wittemyer, G. & Vollrath, F. (2006) Behavioural reactions of elephants towards a dying and deceased matriarch. *Applied Animal Behaviour Science* 100(1–2):87–102. [EMP]
Dounskaia, N. (2005) The internal model and the leading joint hypothesis: Implications for control of multi-joint movements. *Experimental Brain Research* 166:1–16. [ND]
Dounskaia, N. (2010) Control of human limb movements: The leading joint hypothesis and its practical applications. *Exercise and Sport Science Reviews* 38:201–208. [ND]
Dounskaia, N. & Goble, J. (2011) The role of vision, speed and attention in overcoming directional biases during arm movements. *Experimental Brain Research* 209:299–309. [ND]
Dounskaia, N., Goble, J. & Wang, W. (2011) The role of intrinsic factors in control of arm movement direction: Implications from directional preferences. *Journal of Neurophysiology* 105:999–1010. [ND]
Draganski, B. & May, A. (2008) Training-induced structural changes in the adult human brain. *Behavioral Brain Research* 192:137–42. [rKV]
Dufour, V. & Sterck, E. H. M. (2008) Chimpanzees fail to plan in an exchange task but succeed in a tool-using procedure. *Behavioural Processes* 79(1):19–27. [EMP]
Dumontheil, I., Burgess, P. W. & Blakemore, S. J. (2008) Development of rostral prefrontal cortex and cognitive and behavioral disorders. *Developmental Medicine and Child Neurology* 50:168–81. [SRB]
Dunbar, R. (1997) *Grooming, gossip, and the evolution of language.* Harvard University Press. [HIJ]
Dunbar, R. I. M. (1998) The social brain hypothesis. *Evolutionary Anthropology* 6(5): 178–90. [EMP]
Duncker, K. (1945) *On problem solving.* American Psychological Association. [aKV]
Efferson, C., Lalive, R., Richerson, P. J., McElreath, R., & Lubell, M. (2008) Conformists and mavericks: The empirics of frequency-dependent cultural transmission. *Evolution and Human Behavior* 29:56–64. [aKV]
Ehrsson, H. H., Rosén, B., Stockselius, A., Ragnö, C., Köhler, P. & Lundborg, G. (2008) Upper limb amputees can be induced to experience a rubber hand as their own. *Brain* 131:3443–52. [MRL]
Emery, N. J. & Clayton, N. S. (2001) Effects of experience and social context on prospective caching strategies in scrub jays. *Nature* 414:443–46. [AHT]
Emery, N. J. & Clayton, N. S. (2004) The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science* 306:1903–907. [SC]

Enquist, M., Ghirlanda, S., Jarrick, A. & Wachtmeister, C. A. (2008) Why does human culture increase exponentially? *Theoretical Population Biology* 74(1):46–55. [CT, rKV]

Evans, T. A. & Westergaard, G. C. (2006) Self-control and tool-use in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 120(2):163–66. [AB]

Farnè, A., Iriki, A. & Làdavas, E. (2005) Shaping multisensory action-space with tools: Evidence from patients with cross-modal extinction. *Neuropsychologia* 43(2):238–48. [aKV]

Farnè, A. & Làdavas, E. (2000) Dynamic size-change of hand peripersonal space following tool use. *NeuroReport* 11:1645–49. [aKV]

Fay, J. M. & Carroll, R. W. (1994) Chimpanzee tool use for honey and termite extraction in Central Africa. *American Journal of Primatology* 34(4):309–17. [EMP]

Fay, N., Garrod, S. & Carletta, J. (2000) Group discussion as interactive dialogue or as serial monologue: The influence of group size. *Psychological Science* 11(6):481–86. [SR]

Fay, N., Garrod, S. & Roberts, L. (2008) The fitness and functionality of culturally evolved communication systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:351–86. [SR]

Fay, N., Garrod, S., Roberts, L. & Swoboda, N. (2010) The interactive evolution of human communication systems. *Cognitive Science* 34(3):351–86. [SR]

Fitchen, J. (1961) *The construction of Gothic cathedrals: A study of medieval vault erection.* Clarendon Press. [DEM]

Fodor, J. (1987) *Psychosemantics: The problem of meaning in the philosophy of mind*. MIT Press. [GG]

Foley, R. & Lahr, M. M. (2003) On stony ground: Lithic technology, human evolution, and the emergence of culture. *Evolutionary Anthropology* 12:109–22. [MN]

Ford, J. K. B. & Ellis, G. M. (2006) Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Marine Ecology Progress Series* 316:185–99. [EMP]

Foroni, F. & Semin, G. R. (2009) Language that puts you in touch with your bodily feelings: The multimodal responsiveness of affective expressions. *Psychological Science* 20(8):974–80. [HIJ]

Fowler, A. & Sommer, V. (2007) Subsistence technology of Nigerian chimpanzees. *International Journal of Primatology* 28:997–1023. [aKV]

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., & Gomes De Oliveira, M. (2004) Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology* 64(4):359–66. [AB, SC]

Fragaszy, D. & Visalberghi, E. (1989) Social influences on the acquisition of tool-using behaviors in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 103:159–70. [SMR]

Franz, M. & Matthews, L. J. (2010) Social enhancement can create adaptive, arbitrary and maladaptive cultural traditions. *Proceedings of the Royal Society B: Biological Sciences* 277(1698):3363–72. [POJ]

Frey, S. H. (2003) What's so special about human tool use? *Neuron* 39(2):201–204. [aKV]

Frey, S. H. (2004) The neural bases of complex tool use in humans. *Trends in Cognitive Sciences* 8(2):71–78. [aKV]

Frey, S. H. (2007) Neurological specializations for manual gesture and tool use in humans. In: *Evolution of nervous systems*, ed. J. Kaas, pp. 395–406. Elsevier Science. [aKV]

Fujita, K. (2009) A prospect of evolutionary adequacy: Merge and the evolution and development of human language. *Biolinguistics* 3(2–3):128–53. [LB-C]

Gainotti, G. (2006) Anatomical, functional and cognitive determinants of semantic memory disorders. *Neuroscience & Biobehavioral Reviews* 30:577–94. [GG]

Gärdenfors, P. (2001) Slicing the theory of mind. *Danish Yearbook for Philosophy* 36:7–34. [MO]

Gärdenfors, P. (2003) *How Homo became sapiens: On the evolution of thinking.* Oxford University Press. [MO]

Garrod, S. & Doherty, G. (1994) Conversation, coordination and convention – An empirical investigation of how groups establish linguistic conventions. *Cognition* 53(3):181–215. [SR]

Garrod, S., Fay, N., Rogers, S., Walker, B. & Swoboda, N. (2010) Can iterated learning explain the ermergence of graphical symbols? *Interaction Studies* 11(1):33–50. [SR]

Gentner, D. (2003) Why we're so smart. In: *Language in mind: Advances in the study of language and thought*, ed. D. Gentner & S. Goldin-Meadow, pp. 195–235. MIT Press. [DCP]

Gergely, G. (2007) Learning "about" versus learning "from" other minds: Natural pedagogy and its implications. In: *The innate mind: Vol. 3. Foundations and the future*, ed. P. Carruthers, S. Laurence, S. Stich, pp. 170–98. Oxford University Press. [POJ]

Gergely, G. & Csibra, G. (2003) Teleological reasoning in infancy: The naive theory of rational action. *Trends in Cognitive Sciences* 7(7):287–92. [POJ]

Gergely, G. & Csibra, G. (2006) Sylvia's recipe: The role of imitation and pedagogy in the transmission of human culture. In: *Roots of human sociality: Culture, cognition, and human interaction*, ed. N. J. Enfield & S. C. Levinson, pp. 229–55. Berg Publishers. [CT]

Gergely, G., Bekkering, H. & Király, I. (2002) Rational imitation in preverbal infants. *Nature* 415:755–56. [aKV]

German, T. P. & Barrett, H. C. (2005) Functional fixedness in a technologically sparse culture. *Psychological Science* 16(1):1–5. [aKV]

Ghiselin, M. T. (1974) A radical solution to the species problem. *Systematic Zoology* 23(4):536–44. [TN]

Gibson, J. J. (1979) *The ecological approach to visual perception*. Houghton-Mifflin. [rKV]

Gibson, J. J. (1986) *The ecological approach to visual perception*. Erlbaum. [TN]

Gibson, K. (1990) New perspectives on instincts and intelligence: Brain size and the emergence of hierarchical mental constructional skills. In: *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives*, ed. S. Parker & K. Gibson, pp. 97–128. Cambridge University Press. [aKV]

Gibson, K. (1993) General introduction: Animal minds, human minds. In: *Tools, language, and cognition in human evolution*, ed. K. Gibson & T. Ingold, pp. 3–19. Cambridge University Press. [aKV]

Gibson, K. (2007) Putting it all together: A constructionist approach to the evolution of human mental capacities. In: *Rethinking the human revolution*, ed. P. Mellars, K. Boyle, O. Bar-Yosef & C. Stringer, pp. 67–78. McDonald Institute Monographs. [aKV]

Gibson, K. R. (1990) Neurological perspectives on comparative animal and human intelligence: New approaches to the instinct versus learning controversy. In: *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives*, ed. S. Parker & K. Gibson, pp. 97–128. Cambridge University Press. [KRG]

Gibson, K. R. (1991) Tools, language and intelligence, evolutionary implications. *Man* (N.S.) 26:255–64. [KRG]

Gibson, K. R. (1993) Tool use, language and social behavior in relationship to information processing capacities. In: *Tools, language and cognition in human evolution*, ed. K. R. Gibson & T. Ingold, pp. 251–69. Oxford University Press. [KRG]

Gibson, K. R. (1996) The ontogeny and evolution of the brain, cognition and language, In: *Handbook of symbolic intelligence*, ed. A. Lock & C. Peters, pp. 409–33. Oxford University Press. [KRG]

Gibson, K. R. (2002) Evolution of human intelligence: The roles of brain size and mental construction. *Brain, Behavior and Evolution* 59: 10–20. [KRG]

Gibson, K. R. & Jessee, S. (1999) Language evolution and expansions of multiple neural processing areas. In: *The evolution of language: Assessing the evidence from the non-human primates*, ed. B. King, pp. 189–228. School for American Research. [KRG]

Gibson, K. R., Rumbaugh, D. & Beran, M. (2001) Bigger is better: Primate brain size in relationship to cognition. In: *Evolutionary anatomy of the primate cerebral cortex*, ed. D. Falk & K. R. Gibson, pp. 79–97. Cambridge University Press. [KRG]

Goble, J. A., Zhang, Y., Shimansky, Y., Sharma, S. & Dounskaia, N. V. (2007) Directional biases reveal utilization of arm's biomechanical properties for optimization of motor behavior. *Journal of Neurophysiology* 98:1240–52. [ND]

Goel, V. (1995) *Sketches of thought.* MIT Press. [SRB]

Goldberg, A. E. (2003) Constructions: A new theoretical approach to language. *Trends in Cognitive Science* 7(5):219–24. [MAA]

Goldenberg, G., Hartmann-Schmid, K., Sürer, F., Daumüller, M. & Hermsdörfer, J. (2007a) The impact of dysexecutive syndrome on use of tools and technical devices. *Cortex* 43(3):424–35. [aKV]

Goldenberg, G., Hermsdörfer J., Glindemann, R., Rorden, C. & Karnath, H. (2007b) Pantomime of tool use depends on integrity of left inferior frontal cortex. *Cerebral Cortex* 17(12):2769–76. [aKV]

Goldenberg, G. & Spatt, J. (2009) The neural basis of tool use. *Brain* 132:1645–55. [aKV]

Goldin-Meadow, S. (2003) *The resilience of langauge: What gesture creation in deaf children can tell us about how all children learn language.* Psychology Press. [SR]

Goldin-Meadow, S. (2011) What modern-day gesture can tell us about language evolution. In: *Handbook of language evolution*, ed. M. Tallerman & K. R. Gibson, pp. 545–56. Oxford University Press. [KRG]

Gomez, R. L. & Gerken, L. (2000) Infant artificial language learning and language acquisition. *Trends in Cognitive Sciences* 4(5):178–86. [DCP]

Goodall, J. (1998) Learning from the chimpanzees: A message humans can understand. *Science* 282:2184–85. [MN]

Gopnik, A. (2000) Explanation as orgasm and the drive for causal knowledge: The function, evolution, and phenomenology of the theory formation system. In: *Explanation and cognition*, ed. F. Keil & R. Wilson, pp. 299–324. MIT Press. [aKV]

Gopnik, A. & Schulz, L. eds. (2007) *Causal learning: Psychology, philosophy, and computation*. Oxford University Press. [DCP]

Gottlieb, G. (2002) Developmental-behavioral initiation of evolutionary change. *Psychological Review* 109:211–18. [TN]

Gould, S. J. (1977) *Ontogeny and phylogeny*. Belknap. [AB]
Gould, S. J. & Lewontin, R. C. (1979) The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society B: Biological Sciences* 205(1161):581–698. [EMP]
Gould, S. J. & Vrba, E. S. (1982) Exaption – A missing term in the science of form. *Paleobiology* 8(1):4–15. [AB]
Graziano, M. S. (1999) Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National Academy of Sciences* 96:10418–21. [MRL]
Greenfield, P. (1978) Structural parallels between language and action in development. In: *Action, symbol, gesture: The emergence of language*, ed. A. Lock, pp. 415–47. Academic Press. [aKV]
Greenfield, P. (1991) Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences* 14:531–95. [LB-C, aKV]
Greenfield, P. M. (1984) *Mind and media: The effects of television, videogames, and computers*. Harvard University Press. [SR]
Gregory, R. L. (1981) *Mind in science: A history of explanations in psychology and physics*. Cambridge University Press. [POJ]
Grossman, M. (1980) A central processor for hierarchically structured material: Evidence from Broca's aphasia. *Neuropsychologia* 18:299–308. [aKV]
Gruber, A. (1969) A functional definition of primate tool-making. *Man* 4:573–79. [PBC]
Häfner, M. & IJzerman, H. (2011) The face of love: Spontaneous accommodation as social emotion regulation. *Personality and Social Psychology Bulletin*. Published online, retrieved through doi:10.1177/0146167211415629. [HIJ]
Halford, G. S., Wilson, W. H. & Phillips, S. (1998) Processing capacity defined by relational complexity: Implications for comparative, developmental, and cognitive psychology. *Behavioral and Brain Sciences* 21(6):803–31; discussion 831–64. [DCP]
Hansell, M. (2000) *Bird nests and construction behaviour*. Cambridge University Press. [MAA]
Hansell, M. & Ruxton, G. D. (2008) Setting tool use within the context of animal construction behaviour. *Trends in Ecology & Evolution* 23(2):73–78. doi: 10.1016/j.tree.2007.10.006 [MAA, LM]
Hanus, D. & Call, J. (2007) Discrete quantity judgments in the great apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus): The effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology* 21:241–49. [aKV]
Hanus, D., Mendes, N., Tennie, C. & Call, J. (2011) Comparing the performances of apes (*Gorilla gorilla, Pan troglodytes, Pongo pygmaeus*) and human children (*Homo sapiens*) in the floating peanut task. *PLoS ONE* 6(6):e19555. [EMP, AR, rKV]
Hare, B., Call, J. & Tomasello, M. (2001) Do chimpanzees know what conspecifics know? *Animal Behaviour* 61(1):139–51. [AHT]
Hart, D. & Sussman, R. W. (2005) *Man the hunted: Primates, predators, and human evolution*. Westview Press. [PBC]
Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E. & Warren, R. (2009) Primate archaeology. *Nature* 469:339–44. [TN]
Haun, D., Rapold, C. J., Call, J., Janzen, G. & Levinson, S. (2006) Cognitive cladistics and cultural override in hominid spatial cognition. *Proceedings of the National Academy of Sciences* 103(46):17568–73. [rKV]
Haun, D. B. M. & Tomasello, M. (2011) Conformity to peer pressure in preschool children. *Child Development* 82(6):1759–67. [CT]
Hauser, M., Pearson, H. & Seelig, D. (2002) Ontogeny of tool use in cottontop tamarins, *Saguinus oedipus*: Innate recognition of functionally relevant features. *Animal Behaviour* 64(2):299–311. [EMP]
Hauser, M. & Santos, L. (2007) The evolutionary ancestry of our knowledge of tools: From percepts to concepts. In: *Creations of the mind: Theories of artifacts and their representation*, ed. S. Laurence & E. Margolis, pp. 267–88. Oxford University Press. [AB]
Hauser, M. D. (1997) Artifactual kinds and functional design features: What a primate understands without language. *Cognition* 64(3):285–308. [EMP, aKV]
Hauser, M. D., Chomsky, N. & Fitch, W. T. (2002) The faculty of language: What is it, who has it, and how did it evolve? *Science* 298:1569–79. [LB-C, DCP]
Head, H. & Holmes, G. (1911) Sensory disturbances from cerebral lesions. *Brain and Cognition* 34:102–254. [aKV]
Henrich, J. (2002) Decision-making, cultural transmission and adaptation in economic anthropology. In: *Theory in economic anthropology*, ed. J. Ensminger, pp. 251–95. AltaMira Press. [aKV]
Henrich, J. (2004) Demography and cultural evolution: Why adaptive cultural processes produced maladaptive losses in Tasmania. *American Antiquity* 69(2):197–214. [aKV]
Henrich, J. (2009) The evolution of innovation-enhancing institutions. In: *Innovation in cultural systems: Contributions from evolutionary anthropology*, ed. M. O'Brien & S. Shennan, pp. 99–120. MIT Press. [aKV]
Henrich, J. & Gil-White, F. (2001) The evolution of prestige. Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior* 22:165–96. [aKV]
Henrich, J., Heine, S. & Norenzayan, A. (2010) The weirdest people in the world? *Behavioral and Brain Sciences* 33:61–83. [arKV]
Henrich, J. & McElreath, R. (2003) The evolution of cultural evolution. *Evolutionary Anthropology: Issues, News, and Reviews* 12(3):123–35. [aKV]
Henshilwood, C. S. & Marean, C. W. (2003) The origin of modern human behavior. *Current Anthropology* 44:627–51. [LB-C]
Herman, L. M. (2002) Vocal, social, and self-imitation by bottlenosed dolphins. In: *Imitation in animals and artifacts*, ed. K. Dautenhahn & C. Nehaniv, pp. 63–108. MIT Press. [EMP]
Hernik, M. & Csibra, G. (2009) Functional understanding facilitates learning about tools in human children. *Current Opinion in Neurobiology* 19(1):34–38. [aKV]
Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B. & Tomasello, M. (2007) Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science* 317(5843):1360–66. [CT, aKV]
Hewes, G. (1973) Primate communication and the gestural origin of language. *Current Anthropology* 14:5–25. [KRG]
Hewlett, B. S., Fouts, H. N., Boyette, A. H. & Hewlett, B. L. (2011) Social learning among Congo Basin hunter-gatherers. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:1168–78. [MN]
Higuchi, S., Chaminade, T., Imamizua, H. & Kawato, M. (2009) Shared neural correlates for language and tool use in Broca's area. *NeuroReport* 20:1376–81. [arKV, GV]
Hill, K., Barton, M. & Hurtado, A. M. (2009) The emergence of human uniqueness: Characters underlying behavioral modernity. *Evolutionary Anthropology* 18:187–200. [MN]
Hochberg, Z. & Albertsson-Wikland, K. (2008) Evo-devo of infantile and childhood growth. *Pediatric Research* 64:2–7. [MN]
Hockett, C. F. (1960) The origin of speech. *Scientific American* 203:88. [RLH]
Hockings, K., Humle, T., Anderson, J., Biro, D., Sousa, C., Ohashi, G. & Matsuzawa, T. (2007) Chimpanzees share forbidden fruit. *PLoS ONE* 2:e886. [aKV]
Holloway, R. (1969) Culture: A human domain. *Current Anthropology* 10(4):395–412. [RLH, rKV]
Holloway, R. L. (1967) The evolution of the human brain: Some notes toward a synthesis between neural structure and the evolution of complex behavior. *General Systems* 12:3–19. [RLH]
Holloway, R. L. (1975) The role of human social behavior in the evolution of the brain. (*43rd James Arthur Lecture. American Museum of Natural History*, 1973). [RLH]
Holloway, R. L. (1981) Culture, symbols, and human brain evolution: A synthesis. *Dialectical Anthropology* 5:287–303. [RLH]
Holloway, R. L. (1996) Evolution of the human brain. In: *Handbook of symbolic evolution*, ed. A. Lock & C. Peters, pp. 74–116 (chap. 4). Oxford University Press. [RLH]
Holloway, R. L., Yuan, M. S. & Broadfield, D. C. (2004) *Brain endocasts: Paleoneurological evidence, vol. 3, In the human fossil record*, ed. J. Schwartz & I. Tattersall. John Wiley & Sons. [RLH]
Holmes, N. P., Calvert, G. A. & Spence, C. (2004) Extending or projecting peripersonal space with tools? Multisensory interactions highlight only the distal and proximal ends of tools. *Neuroscience Letters* 372:62–67. [aKV]
Holmes, N. P., Calvert, G. A. & Spence, C. (2007) Tool use changes multisensory interactions in seconds: Evidence from the crossmodal congruency task. *Experimental Brain Research* 183:465–76. [MRL]
Holyoak, K. J. & Cheng, P. W. (2011) Causal learning and inference as a rational process: The new synthesis. *Annual Review of Psychology* 62:135–63. [DCP]
Hopkins, W. (2006) Comparative and familial analysis of handedness in great apes. *Psychological Bulletin* 132:538–59. [aKV]
Hopkins, W. D. & Vauclair, J. (2011) Evolution of behavioural and brain asymmetries in primates. In: *Handbook of language evolution*, ed. M. Tallerman & K. R. Gibson, pp. 184–96. Oxford University Press. [KRG]
Hopper, L., Spiteri, A., Lambeth, S., Shapiro, S., Horner, V. & Whiten, A. (2007) Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour* 73:1021–32. [aKV]
Horner, V., Proctor, D., Bonnie, K., Whiten, A. & de Waal, F. (2010) Prestige affects cultural learning in chimpanzees. *PLoS ONE* 5:e10625. [aKV]
Horner, V. & Whiten, A. (2005) Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens). *Animal Cognition* 8(3):164–81. [aKV]
Horner, V., Whiten, A., Flynn, E. & de Waal, F. (2006) Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and

children. *Proceedings of the National Academy of Sciences* 103:13878–83. [aKV]
Hrdy, S. B. (2009) *Mothers and others: The evoltuionary origins of mutual understanding.* Harvard University Press. [SR, aKV]
Hrubesch, C., Preuschoft, S. & van Schaik, C. (2009) Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition* 12:209–16. [SMR]
Hubbard, E. M., Piazza, M., Pinel, P. & Dehaene, S. (2005) Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience* 6(6):435–48. [GV]
Humle, T. & Matsuzawa, T. (2009) Laterality in hand use across four tool-use behaviors among the wild chimpanzees of Bossou, Guinea, West Africa. *American Journal of Primatology* 71:40–48. [aKV]
Hunt, G. R. (1996) Manufacture and use of hook-tools by New Caledonian crows. *Nature* 379(6562):249–51. doi: 10.1038/379249a0 [MAA, AHT]
Hunt, G. R. & Gray, R. D. (2004) The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society B: Biological Sciences* 271(Suppl.):S88–S90. [AHT]
Hunt, K. (2006) Sex differences in chimpanzee foraging behavior and tool use: Implications for the Oldowan. In: *The Oldowan: Case studies into the earliest Stone Age*, ed. K. Schick & N. Toth, pp. 243–66. Stone Age Institute. [aKV]
Hutchins, E. (2008) The role of cultural practices in the emergence of modern human intelligence. *Philosophical Transactions of the Royal Society B* 363(1499):2011–19. [AB]
IJzerman, H. & Semin, G. R. (2009) The thermometer of social relations: Mapping social proximity on temperature. *Psychological Science* 10:1214–20. [HIJ]
Ilyenkov, E. V. (1977) The concept of the ideal. In: *Philosophy in the USSR: Problems of dialectical materialism*, ed. P. N. Fedoseyev, pp. 71–99. Progress. [AR]
Iriki, A. & Sakura, O. (2008) The neuroscience of primate intellectual evolution: Natural selection and passive and intentional niche construction. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:2229–41. [MRL, LM]
Iriki, A., & Taoka, M. (2012). Triadic (ecological, neural, cognitive) niche construction: a scenario of human brain evolution extrapolating tool use and language from the control of reaching actions. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:10–23. [MAA]
Iriki, A., Tanaka, M. & Iwamura, Y. (1996) Coding of modified body schema during tool use by macaque postcentral neurones. *NeuroReport* 7(14):2325–30. [MAA, GAO, aKV]
Isaac, G. L. (1976) Plio-Pleistocene artifact assemblages from East Rudolf, Kenya. In: *Earliest man and environment in the Lake Rudolf Basin: Stratigraphy, paleoecology, and evolution*, ed. Y. Coppens, F. C. Howell, G. L. Isaac & R. Leakey, pp. 552–64. University of Chicago Press. [TN]
Jeffares, B. (2010a) The co-evolution of tools and minds: Cognition and material culture in the hominin lineage. *Phenomenology and the Cognitive Sciences* 9(4):503–20. [BJ]
Jeffares, B. (2010b) The evolution of technical competence: Economic and strategic thinking. Paper presented at the ASCS09: *Proceedings of the 9th Conference of the Australasian Society for Cognitive Science*. Sydney, Australia, October, 2009. From www.maccs.mq.edu.au/news/conferences/2009/ASCS2009/html/jeffares.html. [BJ]
Jensen, K., Hare, B., Call, J. & Tomasello, M. (2006) What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society of London: Series B* 273:1013–21. [aKV]
Jochim, M. A. (1976) *Hunter-Gatherer subsistence and settlement: A predictive model.* Academic Press. [SR]
Jochim, M. A. (1981) *Strategies for survival: Cultural behavior in an ecological context.* Academic Press. [SR]
Johnson-Frey, S. H. (2004) The neural bases of complex tool use in humans. *Trends in Cognitive Sciences* 8:71–78. [DJW]
Jones, S. (2007) Imitation in infancy: The development of imitation. *Psychological Science* 18:593–99. [aKV]
Jones, S. (2009) The development of imitation in infancy. *Philosophical Transactions of the Royal Society B* 364:2325–35. [aKV]
Kaplan, C. A. & Simon, H. A. (1990) In search of insight. *Cognitive Psychology* 22:374–419. [aKV]
Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. (2000) A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology* 4:156–85. [MN, SR]
Kappelman, J. (1996) The evolution of body mass and relative brain size in fossil hominids. *Journal of Human Evolution* 30:243–76. [TN]
Kegl, J., Senghas, A. & Coppola, M. (1999) Creation through contact: Sign language emergence and sign language change in Nicaragua. In: *Language creation and language change: Creolization, diachrony, and development*, pp. 179–238. MIT Press. [SR]
Keil, F. (2011) Science starts early. *Science* 331:1022–23. [aKV]
Kelso, J. A. S. (1995) *Dynamic patterns: The self-organization of brain and behavior.* MIT Press. [AB]
Kemmerer, D. (2006) Action verbs, argument structure constructions, and the mirror neuron system. In: *Action to language via the mirror neuron system*, ed. M. A. Arbib, pp. 347–73. Cambridge University Press. [MAA]
Kempler, D. (1993) Disorders of language and tool use: Neurological and cognitive links. In: *Tools, language, and cognition in human evolution*, ed. K. Gibson & T. Ingold, pp. 193–215. Cambridge University Press. [aKV]
Kendon, A. (1984) Knowledge of sign language in an Australian Aboriginal community. *Journal of Anthropological Research* 40:556–76. [SR]
Kenrick, D. T. & Sheets, V. (1993) Homicidal fantasies. *Ethology and Sociobiology* 14:231–46. [PBC]
Kenward, B., Rutz, C., Weir, A. A. S. & Kacelnik, A. (2006) Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour* 72(6):1329–43. [EMP]
Kenward, B., Weir, A. A. S., Rutz, C. & Kacelnik, A. (2005) Tool manufacture by naive juvenile crows. *Nature* 433:121. [SMR]
Kim, T. W. (2010) Food storage and carrion feeding in the fiddler crab *Uca lactea*. *Aquatic Biology* 10(1):33–39. [EMP]
Kimura, D. (1979) Neuromotor mechanisms in the evolution of human communication. In: *Neurobiology of social communication in primates*, ed. H. Steklis & M. Raleigh, pp. 197–219. Academic Press. [aKV]
Kriegeskorte, N., Mur, M., Ruff, D. A., Kiani, R., Bodurka, J., Esteky, H., Tanaka, K. & Bandettini, P. A. (2008) Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron* 60(6):1126–41. [GG]
Króliczak, G. & Frey, S. H. (2009) A common network in the left cerebral hemisphere represents planning of tool use pantomimes and familiar intransitive gestures at the hand-independent level. *Cerebral Cortex* 19(10):2396–410. [aKV]
Kroliczak, G., Piper, B. J. & Frey, S. H. (2011) Atypical lateralization of language predicts cerebral asymmetries in parietal gesture representations. *Neuropsychologia* 49(7):1698–702. [GV]
Laden, G. & Wrangham, R. W. (2005) The rise of the hominids as an adaptive shift in fallback foods: Plant underground storage organs (USOs) and the origin of australopiths. *Journal of Human Evolution* 49:482–98. [SR]
Lagnado, D. A., Waldmann, M. R., Hagmayer, Y. & Sloman, S. A. (2007) Beyond covariation: Cues to causal structure. In: *Causal learning: Psychology, philosophy, and computation*. ed. A. Gopnik & L. Schulz, pp. 154–72. Oxford University Press. [DCP, aKV]
Laland, K. N. (2004) Social learning strategies. *Learning & Behavior* 32:4–14. [SMR]
Laland, K. N. & Hoppitt, W. (2003) Do animals have culture? *Evolutionary Anthropology* 12:154–72. [aKV]
Laland, K. N., Odling-Smee, J. & Feldman, M. W. (2000) Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences* 23(1):131–46. doi:10.1017/S0140525X00002417. [MAA, PBC]
Leca, J. B., Gunst, N. & Huffman, M. A. (2007) Japanese macaque cultures: Inter- and intra-troop behavioural variability of stone handling patterns across 10 troops. *Behaviour* 144:251–81. [SMR]
Lefebvre, L., Nicolakakis, N. & Boire, D. (2002) Tools and brains in birds. *Behaviour* 139(7):939–73. [MAA, SMR]
Lefebvre, L., Reader, S. M. & Sol, D. (2004) Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution* 63:233–46. [SMR]
Lepre, C. J., Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J.–P., Texier, P.–J., Lenoble, A. & Feibel, C. S. (2011) An earlier origin for the Acheulian. *Nature* 477:82–85. [TN]
Leroi-Gourhan, A. (1964/1993) *Gesture and speech*. MIT Press. [LM]
Lewis, G. (1995) The articulation of circumstance and causal understandings. In: *Causal cognition: A multidisciplinary debate*, ed. D. Sperber, D. Premack & A. Premack, pp. 557–76. Oxford University Press. [aKV]
Lewis, J. W. (2006) Cortical networks related to human use of tools. *Neuroscientist* 12:211–31. [GAO]
Lewis, J. W., Phinney, R. E., Brefczynski-Lewis, J. A. & DeYoe, E. A. (2006) Lefties get it "right" when hearing tool sounds. *Journal of Cognitive Neuroscience* 18:1314–30. [GG]
Lewontin, R. C. (2001) Gene, organism, and environment. In: *Cycles of contingency: Developmental systems and evolution*, ed. S. Oyama, P. E. Griffiths & R. D. Gray, pp. 59–66. MIT Press. [TN]
Lindeyer, C. M. & Reader, S. M. (2010) Social learning of escape routes in zebrafish and the stability of behavioural traditions. *Animal Behaviour* 79:827–34. [SMR]
Locke, J. L. & Bogin, B. (2006) Language and life history: A new perspective on the development and evolution of human language. *Behavioral and Brain Sciences* 29:259–325. [MN]
Longo, M. R. & Lourenco, S. F. (2006) On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia* 44:977–81. [MRL]
Lonsdorf, E. & Hopkins, W. (2005) Wild chimpanzees show population-level handedness for tool use. *Proceedings of the National Academy of Sciences* 102:12634–38. [aKV]

Lycett, S. & Gowlett, J. (2008) On questions surrounding the Acheulean "tradition." *World Archaeology* 40:295–315. [aKV]

Lycett, S. J. & Cramon-Taubadel, N. V. (2008) Acheulean variability and hominin dispersals: A model-bound approach. *Journal of Archaeological Science* 35(3):553–62. [BJ]

Lycett, S. J. & Gowlett, J. A. J. (2008) On questions surrounding the Acheulean 'Tradition.' *World Archaeology* 40(3):295–315. [BJ]

Lyons, D. E., Young, A. G. & Keil, F. C. (2007) The hidden structure of overimitation. *Proceedings of the National Academy of Sciences* 104:19751–56. [CT, aKV]

Macchiarelli, R., Bondioli, L., Debénath, A., Mazurier, A., Tournepiche, J.-F., Birch, W. & Dean, M. C. (2006) How Neanderthal molar teeth grew. *Nature* 444:748–51. [MN]

MacLarnon, A. (1996) The scaling of gross dimensions of the spinal cord in primates and other species. *Journal of Human Evolution* 30:71–87. [aKV]

Malafouris, L. (2008) Beads for a plastic mind: The "blind man's stick" (BMS) hypothesis and the active nature of material culture. *Cambridge Archaeological Journal* 18:401–14. [LM]

Malafouris, L. (2010a) Knapping intentions and the marks of the mental. In: *The cognitive life of things: Recasting the boundaries of the mind*, ed. L. Malafouris & C. Renfrew, pp. 13–22. McDonald Institute Monographs. [LM]

Malafouris, L. (2010b) The brain-artefact interface (BAI): A challenge for archaeology and cultural neuroscience. *Social Cognitive and Affective Neuroscience* 5(2–3):264–73 (10.1093/scan/nsp057). [LM]

Marasco, P. D., Kim, K., Colgate, J. E., Peshkin, M. A. & Kuiken, T. A. (2011) Robotic touch shifts perception of embodiment to a prosthesis in targeted reinnervation amputees. *Brain* 134:747–58. [MRL]

Maravita, A. & Iriki, A. (2004) Tools for the body (schema). *Trends in Cognitive Sciences* 8(2):79–86. [aKV]

Maravita, A., Husain, M., Clarke, K. & Driver, J. (2001) Reaching with a tool extends visual-tactile interactions into far space: Evidence from cross–modal extinction. *Neuropsychologia* 39:580–85. [aKV]

Maravita, A., Spence, C., Kennett, S. & Driver, J. (2002) Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition* 83:25–34. [aKV]

Marlowe, F. (2007) Hunting and gathering: The human sexual division of foraging labor. *Cross-Cultural Research* 41:170–95. [aKV]

Marshall-Pescini, S. & Whiten, A. (2008) Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: An experimental approach. *Animal Cognition* 11:449–56. [SMR]

Martin-Ordas, G. & Call, J. (2009) Assessing generalization within and between trap tasks in the great apes. *International Journal of Comparative Psychology* 22:43–60. [aKV]

Martin-Ordas, G., Call, J. & Colmenares, F. (2008) Tubes, tables and traps: Great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition* 11(3):423–30. [aKV]

Matsuzawa, T. (2001) *Primate origins of human cognition and behavior.* Springer Tokyo. [aKV]

Matsuzawa, T. (2009) Symbolic representation of number in chimpanzees. *Current Opinion in Neurobiology* 19:92–98. [aKV]

McClelland, D. (1985) *Human motivation.* Scott Foresman. [aKV]

McCowan, B., Marino, L., Vance, E., Walke, L. & Reiss, D. (2000) Bubble ring play of bottlenose dolphins (*Tursiops truncatus*): Implications for cognition. *Journal of Comparative Psychology* 114(1):98–105. [EMP]

McElreath, R. (2010) The coevolution of genes, innovation and culture in human evolution. In: *Mind the gap*, ed. P. Kappeler & J. Silk, pp. 451–74. Springer. [aKV]

McGrew, W. (1974) Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution* 3(6):501–508. [EMP]

McGrew, W. (1992) *Chimpanzee material culture: Implications for human evolution.* Cambridge University Press. [SC, aKV]

McGrew, W. (1993) The intelligent use of tools: Twenty propositions. In: *Tools, language, and cognition in human evolution*, ed. K. Gibson & T. Ingold, pp. 151–69. Cambridge University Press. [arKV]

McGrew, W. C. & Marchant, L. F. (1999) Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates* 40:509–13. [aKV]

McGrew, W. C. & Tutin, C. E. G. (1972) Chimpanzee dentistry. *Journal of the American Dental Association* 85:1198–204. [DEM]

McGuigan, N., Whiten, A., Flynn, E. & Horner, V. (2007) Imitation of causally opaque versus causally transparent tool use by 3- and 5-year-old children. *Cognitive Development* 22:353–64. [aKV]

McNabb, J., Binyon, F. & Hazelwood, L. (2004) The large cutting tools from the South African Acheulean and the question of social traditions. *Current Anthropology* 45(5):653–77. [BJ]

McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., Bobe, R. & Béarat, H. A. (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466:857–60. [TN]

Melis, A., Hare, B. & Tomasello, M. (2008) Do chimpanzees reciprocate received favours? *Animal Behaviour* 76:951–62. [aKV]

Menary, R. (2010) *The extended mind.* MIT Press. [BJ]

Mendes, N., Hanus, D. & Call, J. (2007) Raising the level: Orangutans use water as a tool. *Biology Letters* 3:453–55. [AR]

Mercader, J., Panger, M. & Boesch, C. (2002) Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296:1452–55. [SC]

Mesoudi, A. (2009) How cultural evolutionary theory can inform social psychology, and vice versa. *Psychological Review* 116:929–52. [aKV]

Mesoudi, A. (2011a) Variable cultural acquisition costs constrain cumulative cultural evolution. *PLoS ONE* 6(3): e18239 [aKV]

Mesoudi, A. (2011b) An experimental comparison of human social learning strategies: Payoff-biased social learning is adaptive but underused. *Evolution and Human Behavior* 32(5): 334–42. [aKV]

Michel, G. & Harkins, D. (1985) Concordance of handedness between teacher and student facilitates learning manual skills. *Journal of Human Evolution* 14:597–601. [aKV]

Miller, G. A., Gallanter, E. & Pribram, K. H. (1960) *Plans and the structure of behavior.* Holt. [RLH]

Mithen, S. (1994) Technology and society during the Middle Pleistocene: Hominid group size, social learning and industrial variability. *Cambridge Archaeological Journal* 4:3–32. [aKV]

Mithen, S. (1996) *The prehistory of the mind: The cognitive origins of art and science.* Thomas and Hudson. [aKV]

Mithen, S. (1999) Imitation and cultural change: A view from the Stone Age, with specific reference to the manufacture of handaxes. In: *Mammalian social learning: Comparative and ecological perspectives*, ed. H. Box & K. Gibson, pp. 389–99. Cambridge University Press. [aKV]

Mokyr, J. (2002) *The gifts of Athena: Historical origins of the knowledge economy.* Princeton University Press. [aKV]

Moll, H. & Tomasello, M. (2007) Cooperation and human cognition: The Vygotskian intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362(1480):639–48. [CT]

Moore, A., Hillman, G. & Legge, A. (2000) *Village on the Euphrates: From foraging to farming at Abu Hureyra.* Oxford University Press. [aKV]

Morand-Ferron, J., Lefebvre, L., Reader, S. M., Sol, D. & Elvin, S. (2004) Dunking behaviour in Carib grackles. *Animal Behaviour* 68:1267–74. [SMR]

Morris, M. W., Nisbett, R. E. & Peng, K. (1995) Causal attribution across domains and cultures. In: *Causal cognition: A multidisciplinary debate*, ed. D. Sperber, D. Premack & A. Premack, pp. 577–614. Oxford University Press. [aKV]

Morrison, R., Krawczyk, D., Holyoak, K., Hummel, J., Chow, T., Miller, B. & Knowlton, B. (2004) A neurocomputational model of analogical reasoning and its breakdown in frontotemporal lobar degeneration. *Journal of Cognitive Neuroscience* 16:260–71. [aKV]

Mulcahy, N. J. & Call, J. (2006a) How great apes perform on a modified trap-tube task. *Animal Cognition* 9:193–99. [rKV, AHT]

Mulcahy, N. J. & Call, J. (2006b) Apes save tools for future use. *Science* 312:1038–40. [aKV]

Murray, C. D. (2004) An interpretative phenomenological analysis of the embodiment of artificial limbs. *Disability and Rehabilitation* 26:963–73. [MRL]

Nagell, K., Olguin, K. & Tomasello, M. (1993) Processes of social learning in the tool use of chimpanzees and human children. *Journal of Comparative Psychology* 107:174–86. [CT]

Nakamura, M. & Itoh, N. (2001) Sharing of wild fruits among male chimpanzees: Two cases from Mahale, Tanzania. *Pan-African News* 8:28–31. [aKV]

Naqshbandi, M. & Roberts, W. (2006) Anticipation of future events in squirrel monkeys (Saimiri sciureus) and rats (Rattus norvegicus): Tests of the Bischof-Köhler hypothesis. *Journal of Comparative Psychology* 120:345–57. [aKV]

Nelson, E. L., Berthier, N. E., Metevier, C. M. & Novak, M. A. (2010) Evidence for motor planning in monkeys: Rhesus macaques select efficient grips when transporting spoons. *Developmental Science* 14:822–31. [DJW]

Nielsen, M. (2009) The imitative behavior of children and chimpanzees: A window on the transmission of cultural traditions. *Revue de Primatologie* 1:5. [CT]

Nielsen, M. (2012) Imitation, pretend play and childhood: Essential elements in the evolution of human culture? *Journal of Comparative Psychology* 126:170–81. doi:10.1037/a0025168 [MN]

Nielsen, M. & Blank, C. (2011) Imitation in young children: When who gets copied is more important than what gets copied. *Developmental Psychology* 47:1050–53. [MN]

Nielsen, M., Simcock, G. & Jenkins, L. (2008) The effect of social engagement on 24-month-olds' imitation from live and televised models. *Developmental Science* 11:722–31. [CT]

Nielsen, M. & Tomaselli, K. (2010) Over-imitation in Kalahari Bushman children and the origins of human cultural cognition. *Psychological Science* 21:729–36. [MN]

Nonaka, T., Bril, B. & Rein, R. (2010) How do stone knappers predict and control the outcome of flaking? Implications for understanding early stone tool technology. *Journal of Human Evolution* 59:155–67. [TN]

Norenzayan, A. & Nisbett, R. E. (2000) Culture and causal cognition. *Current Directions in Psychological Science* 9:132–35. [aKV]
Norman, D. A. (1988) *The psychology of everyday things.* Basic Books. [POJ, rKV]
Noser, R. & Byrne, R. W. (2010) How do wild baboons (*Papio ursinus*) plan their routes? Travel among multiple high-quality food sources with inter-group competition. *Animal Cognition* 13(1):145–55. [EMP]
Nowak, M. & Sigmund, K. (2005) Evolution of indirect reciprocity. *Nature* 437:1291–98. [aKV]
Nunn, C. L. & Barton, R. A. (2001) Comparative methods for studying primate adaptation and allometry. *Evolutionary Anthropology* 10:81–96. [SMR]
Ochipa, C., Rothi, L. & Heilman, K. (1992) Conceptual apraxia in Alzheimer's disease. *Brain* 115:1061–71. [aKV]
O'Connell, J., Hawkes, K. & Blurton Jones, N. (2002) Meat-eating, grandmothering, and the evolution of early human diets. In: *Human diet: Its origin and evolution*, ed. P. S. Ungar & M. F. Teaford, pp. 49–60. Bergin & Garvey. [SR]
Odling-Smee, F. J., Laland, K. N. & Feldman, M. W. (2003) *Niche construction: The neglected process in evolution*. Princeton University Press. [TN]
Orban, G. A., Claeys, K., Nelissen, K., Smans, R., Sunaert, S., Todd, J. T., Wardak, C., Durand, J. & Vanduffel, W. (2006) Mapping the parietal cortex of human and non-human primates. *Neuropsychologia* 44(13):2647–67. [GAO, arKV, GV]
Osvath, M. (2008) Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology* 19(5):190–91. [EMP]
Osvath, M. (2010) Great ape foresight is looking great. *Animal Cognition* 13(5):177–81. [MO, rKV]
Osvath, M. & Osvath, H. (2008) Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: Self-control and pre-experience in the face of future tool use. *Animal Cognition* 11(4):661–74. [MO, EMP, arKV]
Over, H. & Carpenter, M. (2009) Priming third-party ostracism increases affiliative imitation in children. *Developmental Science* 12:F1–F8. [CT]
Over, H. & Carpenter, M. (2011) Putting the social into social learning: Explaining both selectivity and fidelity in children's copying behavior. *Journal of Comparative Psychology* Advance online publication. doi: 10.1037/a0024555 [CT]
Overington, S. E., Morand-Ferron, J., Boogert, N. J. & Lefebvre, L. (2009) Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour* 78(4):1001–10. [SMR]
Parker, S. T. & Gibson, K. R. (1979) A model of the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences* 2:367–407. [KRG]
Patterson, E. M. & Mann, J. (2011) The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (*Tursiops* sp.). *PLoS ONE* 6(7):e22243. [EMP, SMR]
Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G. & Orban, G. A. (2009) The representation of tool use in humans and monkeys: Common and uniquely human features. *The Journal of Neuroscience* 29(37):11523–39. PMID: 19759300. [GAO, rKV]
Penn, D. C. & Povinelli, D. J. (2007a) Causal cognition in human and nonhuman animals: A comparative, critical review. *Annual Review of Psychology*. 58:97–118. [DCP, aKV]
Penn, D. C. & Povinelli, D. J. (2007b) On the lack of evidence that non-human animals possess anything remotely resembling a "theory of mind." *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:731–44. [AHT, arKV]
Penn, D. C., Holyoak, K. & Povinelli, D. J. (2008) Darwin's mistake: Explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences* 31(2):109–78. [LM, DCP, AHT, arKV]
Petraglia, M., Shipton, C. & Paddayya, K. (2005) Life and mind in the Acheulean: A case study from India. In: *The hominid individual in context: Archaeological investigations of Lower and Middle Pleistocene landscapes, locales and artefacts*, ed. C. Gamble & M. Porr, pp. 197–219. Routledge. [aKV]
Pinel, P. & Dehaene, S. (2010) Beyond hemispheric dominance: Brain regions underlying the joint lateralization of language and arithmetic to the left hemisphere. *Journal of Cognitive Neuroscience* 22(1):48–66. [GV]
Pinker, S. (2010) The cognitive niche: Coevolution of intelligence, sociality, and language. *Proceedings of the National Academy of Sciences* 107(Suppl 2):8993–99. [AB]
Pinker, S. & Jackendoff, R. (2005) The faculty of language: What's special about it? *Cognition* 95:201–36. [DCP]
Plotkin, H. C., ed. (1988) *The role of behavior in evolution*. MIT Press. [TN]
Plotnik, J. M., de Waal, F. B. M., Moore, D. & Reiss, D. (2010) Self-recognition in the Asian elephant and future directions for cognitive research with elephants in zoological settings. *Zoo Biology* 29(2):179–91. [EMP]
Plotnik, J. M., Lair, R., Suphachoksahakun, W. & de Waal, F. B. M. (2011) Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Science* 108(12):5116–21. [EMP]
Plummer, T. (2004) Flaked stones and old bones: Biological and cultural evolution at the dawn of technology. *Yearbook of Physical Anthropology* 47:118–64. [TN]
Povinelli, D. J. & Dunphy-Lelii, S. (2001) Do chimpanzees seek explanations? Preliminary comparative investigations. *Canadian Journal of Experimental Psychology* 55(2):187–95. [aKV]
Povinelli, D. J., Reaux, J. E. & Frey, S. H. (2010) Chimpanzees' context-dependent tool use provides evidence for separable representations of hand and tool even during active tool use within peripersonal space. *Neuropsychologia* 48:243–47. [MRL, aKV]
Povinelli, D. J., Reaux, J.E., Theall, L.A. & Giambrone, S. (2000) *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford University Press. [AB, SC, DCP, arKV]
Povinelli, D. J. & Vonk, J. (2003) Chimpanzee minds: Suspiciously human? *Trends in Cognitive Sciences* 7:157–60. [aKV]
Powell, A., Shennan, S. & Thomas, M. (2009) Late Pleistocene demography and the appearance of modern human behavior. *Science* 324:1298–301. [aKV]
Premack, D. (2004) Is language the key to human intelligence? *Science* 303:318–20. [aKV]
Premack, D. & Premack, A. (1994) Levels of causal understanding in chimpanzees and children. *Cognition* 50:347–62. [aKV]
Premack, D. & Woodruff, G. (1978) Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences* 1:515–26. [MO, aKV]
Preston, S. & de Waal, F. (2002) Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences* 25:1–20. [MO]
Preuschoft, S. & Van Hooff, J. A. R. A. M. (1997) The social function of "smile" and "laughter": Variations across primate species and societies. In: *Non-verbal communication: Where nature meets culture*, ed. U. Segerstrale & P. Molnàr, pp. 171–89. Erlbaum. [HIJ]
Pruetz, J. D. & Bertolani, P. (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology* 17(5):412–17. [EMP]
Pulvermüller, F. (2005) Brain mechanisms linking language and action. *Nature Reviews Neuroscience* 6: 576–82. [HIJ]
Quallo, M. M., Price, C. J., Ueno, K., Asamizuya, T., Cheng, K., Lemon, R. N. & Iriki, A. (2009) Gray and white matter changes associated with tool-use learning in macaque monkeys. *Proceedings of the National Academy of Sciences* 106:18379–84. [MRL, rKV]
Quartz, S. R. & Sejnowski, T. J. (1997) The neural basis of cognitive development: A constructivist manifesto. *Behavioral and Brain Sciences* 20(4):537–56. [BJ]
Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. (2007) Planning for the future by Western Scrub-Jays. *Nature* 445:919–21. [AHT, aKV]
Ragir, S. (1985) Retarded development: The evolutionary mechanism underlying the emergence of the human capacity for language. *The Journal of Mind and Behavior* 6(4):451–68. [SR]
Ragir, S. (2000) Diet and food preparation: Rethinking early hominid behavior. *Evolutionary Anthropology* 9(4):153–56. [SR]
Ragir, S. (2002) Constraints on communities with indigenous sign languages: Clues to the dynamics of language genesis. In: *Transitions to language*, ed A. Wray, pp. 272–94. Oxford University Press. [SR]
Ragir, S., Rosenberg, M. & Tierno, P. (2000) Gut morphology and the avoidance of carrion among chimpanzees, baboons and early hominids. *Journal of Anthropological Research* 56(4):477–512. [SR]
Rakoczy, H. (2008) Pretence as individual and collective intentionality. *Mind and Language* 23:499–517. [AR]
Rakoczy, H., Warneken, F. & Tomasello, M. (2008) The sources of normativity: Young children's awareness of the normative structure of games. *Developmental Psychology* 44:875–81. [CT]
Rappaport, R. A. (1979) Sanctity and lies in evolution. In: *Ecology, meaning and religion*, ed. R. A. Rappaport, pp. 223–46. North Atlantic Books. [DEM]
Raymond, M. & Pontier, D. (2004) Is there geographical variation in human handedness? *Laterality* 9:35–51. [aKV]
Reader, S. M. & Laland, K. N. (2002) Social intelligence, innovation and enhanced brain size in primates. *Proceedings of the National Academy of Sciences* 99:4436–41. [EMP, SMR]
Reader, S. M. & Laland, K. N., eds. (2003) *Animal innovation*. Oxford University Press. [SMR]
Reader, S. M., Hager, Y. & Laland, K. N. (2011) The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:1017–27. [SMR, rKV]
Reed, E. S. (1985) An ecological approach to the evolution of behavior. In: *Issues in the ecological study of learning*, ed. T. Johnston & A. Pietrewicz, pp. 357–83. Erlbaum. [TN]
Reed, E. S. (1996) *Encountering the world: Toward an ecological psychology*. Oxford University Press. [TN]
Reiff, D. D. (1971) Viollet le Duc and historic restoration: The west portals of Notre-Dame. *Journal of the Society of Architectural Historians* 30(1):17–30. [DEM]

Richerson, P. & Boyd, R. (2005) *Not by genes alone: How culture transformed human evolution.* University of Chicago Press. [PBC, HIJ, aKV]
Richerson, P. & Boyd, R. (2008) Response to our critics. *Biology & Philosophy* 23:301–15. [aKV]
Rightmire, G. (2004) Brain size and encephalization in early to mid-Pleistocene *Homo. American Journal of Physical Anthropology* 124:109–23. [aKV]
Rivkin, J. (2000) Imitation of complex strategies. *Management Science* 46(6):824–44. [rKV]
Rizzo, A. (2000) La natura degli artefatti e la loro progettazione. *Sistemi Intelligenti* 12:437–52. [AR]
Rizzo, A. (2006) The origin and design of intentional affordances. In: *Proceedings of the 6th Conference on Designing Interactive Systems*, pp. 239–40. ACM Press. [AR]
Rizzo, A. & Bacigalupo, M. (2004) Scenarios: Heuristics for action. In: *Proceedings of XII European Conference on Cognitive Ergonomics, Living and Working with Technology*, ed. D. J. Reed, G. Baxter & M. Blythe, pp. 153–60. EACE. [AR]
Rizzolatti, G. & Arbib, M. A. (1998) Language within our grasp. *Trends in Neurosciences* 21(5):188–94. [LB-C, aKV]
Rizzolatti, G. & Craighero, L. (2004) The mirror-neuron system. *Annual Review of Neuroscience* 27:169–92. [GAO]
Robin, N. & Holyoak, K. J. (1995) Relational complexity and the functions of the prefrontal cortex. In: *The cognitive neurosciences*, ed. M. Gazzaniga, pp. 987–97. MIT Press. [DCP]
Roche, H. (2005) From simple flaking to shaping: Stone-knapping evolution among early hominins. In: *Stone knapping: The necessary conditions for a uniquely hominin behaviour*, ed. V. Roux & B. Bril, pp. 35–48. McDonald Institute for Archaeological Research. [TN]
Rosen, R. (2000) *Essays on life itself.* Columbia University Press. [TN]
Rosenbaum, D. A. (2010) *Human motor control, 2d ed.* Academic Press/Elsevier. [DJW]
Rosenbaum, D. A., Cohen, R. G., Meulenbroek, R. G. & Vaughan, J. (2006) Plans for grasping objects. In: *Motor control and learning over the lifespan*, ed. M. Latash & F. Lestienne, pp. 9–25. Springer. [DJW]
Rosenbaum, D. A, van Heugten, C. M. & Caldwell, G. E. (1996) From cognition to biomechanics and back: The end-state comfort effect and the middle-is-faster effect. *Acta Psychologica* 94(1):59–85. [POJ]
Rosenbaum, D. A., Marchak, F., Barnes, H. J., Vaughan, J., Slotta, J. & Jorgensen, M. (1990) Constraints for action selection: Overhand versus underhand grips. In: *Attention and performance XIII: Motor representation and control*, ed. M. Jeannerod, pp. 321–42. Erlbaum. [DJW]
Roser, M., Fugelsang, J., Dunbar, K., Corballis, P. & Gazzaniga, M. (2005) Dissociating processes supporting causal perception and causal inference in the brain. *Neuropsychology* 19:591–602. [aKV]
Rossano, M. (2003) Expertise and the evolution of consciousness. *Cognition* 89:207–36. [aKV]
Rubinov, M. & Sporns, O. (2010) Complex network measures of brain connectivity: Uses and interpretations. *Neuroimage* 52(3):1059–69. [GV]
Rumelhart, D. E., McClelland, J. L. & the PDP Research Group. (1986) *Parallel distributed processing: Explorations in the microstructure of cognition, vol. 1.* MIT Press. [AB]
Rusbult, C. E., Verette, J., Whitney, G. A., Slovik, L. F. & Lipkus, I. (1991) Accommodation processes in close relationships: Theory and preliminary empirical evidence. *Journal of Personality and Social Psychology* 60(1):53–78. [HIJ]
Santos, L. R., Miller, C. T. & Hauser, M. D. (2003) Representing tools: How two non-human primate species distinguish between the functionally relevant and irrelevant features of a tool. *Animal Cognition* 6(4):269–81. [AB, EMP, rKV]
Sanz, C. & Morgan, D. (2007) Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution* 52:420–33. [aKV]
Sanz, C. & Morgan, D. (2010) Complexity of chimpanzee tool using behaviors. In: *The mind of the chimpanzee: Ecological and experimental perspectives*, ed. E. V. Lonsdorf, S. R. Ross & T. Matsuzawa, pp. 127–40. University of Chicago Press. [AB, rKV]
Sanz, C., Schning, C. & Morgan, D. (2009) Chimpanzees prey on army ants with specialized tool set. *American Journal of Primatology* 71:1–8. [aKV]
Saviotti, P. (1996) *Technological evolution, variety and the economy.* Edward Elgar. [aKV]
Saviotti, P. & Metcalfe, J. (1984) A theoretical approach to the construction of technological output indicators. *Research Policy* 13:141–51. [aKV]
Schick, K. & Toth, N. (1993) *Making silent stones speak: Human evolution and the dawn of technology.* Simon and Schuster. [RLH]
Schiffer, M. B. & Miller, A. (1999) *The material life of human beings: Artifacts, behavior, and communication.* Routledge. [LM]
Schmelz, M., Call, J. & Tomasello, M. (2011) Chimpanzees know that others make inferences. *Proceedings of the National Academy of Sciences* 108:17284–89. [AHT]
Schulz, L., Gopnik, A. & Glymour, C. (2007) Preschool children learn about causal structure from conditional interventions. *Developmental Science* 10:322–32. [aKV]
Searle, J. (1995) *The construction of social reality.* Free Press. [AR]
Seed, A. & Byrne, R. (2010) Animal tool-use. *Current Biology* 20:1032–39. [LM]
Seed, A. M., Call, J., Emery, N. J. & Clayton, N. S. (2009) Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology: Animal Behavior Processes* 35:23–34. [AHT, arKV]
Sellen, D. W. & Smay, D. B. (2001) Relationship between subsistence and age at weaning in "preindustrial" societies. *Human Nature* 12:47–87. [MN]
Semaw, S., Renne, P. R., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N. & Mowbray, K. (1997) 2.5 million-year-old stone tools from Gona, Ethiopia. *Nature* 385:333–36. [TN]
Senghas, R. J., Senghas, A. & Pyers, J. E. (2005) The emergence of Nicaraguan sign language: Questions of development, acquisition, and evolution. In *Biology and knowledge revisited: From neurogenesis to psychogenesis*, ed. J. Langer, S. T. Parker & C. Milbrath, pp. 287–306. Erlbaum. [SR]
Seppänen, J. T., Forsman, J. T., Mönkkönen, M., Krams, I. & Salmi, T. (2011) New behavioural trait adopted or rejected by observing heterospecific tutor fitness. *Proceedings of the Royal Society B: Biological Sciences* 278:1736–41. [SMR]
Serino, A., Bassolino, M., Farnè, A. & Làdavas, E. (2007) Extended multisensory space in blind cane users. *Psychological Science* 18:642–48. [MRL]
Sharon, G. (2009) Acheulian giant-core technology: A worldwide perspective. *Current Anthropology* 50(3):335–67. [BJ]
Shennan, S. & Steele, J. (1999) Cultural learning in hominids: A behavioural ecological approach. In: *Mammalian social learning: Comparative and ecological perspectives*, ed. H. Box & K. Gibson, pp. 367–88. Cambridge University Press. [aKV]
Shipton, C. (2010) Imitation and shared intentionality in the Acheulean. *Cambridge Archaeological Journal* 20:197–210. [aKV]
Shubin, N. & Marshall C. (2000) Fossils, genes and the origin of novelty. *Paleobiology* 26(4):324–40. Supplement. [AB]
Shumaker, R. W., Walkup, K. R. & Beck, B. B. (2011) *Animal tool behavior.* The Johns Hopkins University Press. [SC, SMR]
Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A., Lambeth, S., Mascaro, J. & Schapiro, S. (2005) Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437:1357–59. [aKV]
Silva, F. J., Page, D. M. & Silva, K. M. (2005) Methodological-conceptual problems in the study of chimpanzees' folk physics: How studies with adult humans can help. *Learning and Behavior* 33:47–58. [AHT]
Simon, H. (1996) *Sciences of the artificial*, 3rd ed. MIT Press. [AB]
Simonton, D. K. (2003) Human creativity: Two Darwinian analyses. In: *Animal innovation*, ed. S. M. Reader & K. N. Laland, pp. 309–25. Oxford University Press. [SMR]
Sirigu, A., Cohen, L., Duhamel, J. R., Pillon, B., Dubois, B. & Agid, Y. (1995) A selective impairment of hand posture for object utilization in apraxia. *Cortex* 31:41–55. [aKV]
Slocombe, K. (2011) Have we underestimated great ape vocal capacities? In: *Handbook of language evolution*, ed. M. Tallerman & K. R. Gibson, pp. 90–95. Oxford University Press. [KRG]
Slocombe, K. & Newton-Fisher, N. (2005) Fruit sharing between wild adult chimpanzees (Pan troglodytes schweinfurthii): A socially significant event? *American Journal of Primatology* 65:385–91. [aKV]
Smith, S. (1995) Getting into and out of mental ruts: A theory of fixation, incubation, and insight. In: *The nature of insight*, ed. R. J. Sternberg & J. Davidson, pp. 229–51. MIT Press. [aKV]
Smith, T. M., Tafforeau, P., Reid, D. J., Pouech, J., Lazzari, V., Zermeno, J. P., Guatelli-Steinberg, D., Olejniczak, A. J., Hoffman, A., Radovcic, J., Makaremi, M., Toussaint, M., Stringer, C. & Hublin, J.-J. (2010) Dental evidence for ontogenetic differences between modern humans and Neanderthals. *Proceedings of the National Academy of Sciences* 107:20923–28. [MN]
Sofer, O., Adovasio, J. M., Illingworth, J. S., Amirkhanov, K. A., Praslov, N. D. & Street, M. (2000) Paleolithic perishables made permanent. *Antiquity* 74:812–21. [LB-C]
Stanford, C. B. (2001) A comparison of social meat-foraging by chimpanzees and human foragers. In: *Meat-eating and human evolution*, ed. C. B. Stanford & H. T. Bunn, pp. 122–40. Oxford University Press. [aKV]
Stanford, C. B., Wallis, J., Mpongo, E. & Goodall, J. (1994) Hunting decisions in wild chimpanzees. *Behaviour* 131:1–20. [aKV]
Steels, L. (2006) Experiments on the emergence of human communication. *Trends in Cognitive Sciences* 10(8):347–49. [SR]
Steels, L., Kaplan, F., Mcintyre, A. & Van Looveren, J. (2002) Crucial factors in the origins of word-meaning. In: *The transitions to language*, ed. A. Wray, pp. 252–71. Oxford University Press. [SR]
Sterelny, K. (2003a) Cognitive load and human decision, or, three ways of rolling the rock uphill. In: *The innate mind: Vol. 2. Culture and cognition*, ed. P. Carruthers, S. Laurence, S. Stich, pp. 218–33. Oxford University Press. [POJ]

Sterelny, K. (2003b) *Thought in a hostile world: The evolution of human cognition*. Blackwell Publishing. [AB, BJ, POJ]
Sterelny, K. (2006) The evolution and evolvability of culture. *Mind and Language* 21:137–65. [aKV]
Sterelny, K. (2010a) Minds: Extended or scaffolded? *Phenomenology and the Cognitive Sciences* 9(4):465–81. [BJ]
Sterelny, K. (2010b) The evolved apprentice. From http://onthehuman.org/2010/08/the-evolved-apprentice/. [BJ]
Sterelny, K. (2012) *The evolved apprentice: The 2008 Jean Nicod Lectures.* MIT Press. [BJ]
Stevens, J. & Hauser, M. (2004) Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences* 8:60–65. [aKV]
Stewart, F. A., Piel, A. K. & McGrew, W. C. (2011) Living archaeology: Artefacts of specific nest site fidelity in wild chimpanzees. *Journal of Human Evolution* 61(4):388–95. doi: 10.1016/j.jhevol.2011.05.005 [MAA]
Stiegler, B. (1998) *Technics and time, 1. The fault of epimetheus*. Stanford University Press. [LM]
Stoet, G. & Snyder, L. H. (2003) Executive control and task-switching in monkeys. *Neuropsychologia* 41:1357–64. [GS]
Stoet, G. & Snyder, L. H. (2004) Single neurons in posterior parietal cortex (PPC) of monkeys encode cognitive set. *Neuron* 42:1003–12. [GS]
Stoet, G. & Snyder, L. H. (2007) Extensive practice does not eliminate human switch costs. *Cognitive, Affective, & Behavioral Neuroscience* 7:192–97. [GS]
Stoet, G. & Snyder, L. H. (2009) Neural correlates of executive control functions in the monkey. *Trends in Cognitive Sciences* 13:228–34. [GS]
Stokes, E. & Byrne, R. (2001) Cognitive capacities for behavioural flexibility in wild chimpanzees (Pan troglodytes): The effect of snare injury on complex manual food processing. *Animal Cognition* 4:11–28. [aKV]
Stokoe, W. (2001) *Language in hand: Why sign came before speech.* Gallaudet University Press. [aKV]
Stout, D. (2011) Stone toolmaking and the evolution of human culture and cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:1050–59. [MAA, rKV]
Stout, D. & Chaminade, T. (2007) The evolutionary neuroscience of tool making. *Neuropsychologia* 45(5):1091–100. [arKV]
Stout, D., Semaw, S., Rogers, M. J. & Cauche, D. (2010) Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution* 58:474–91. [TN]
Stout, D., Toth, N. & Schick, K. (2010) Understanding Oldowan knapping skill: An experimental study of skill acquisition in modern humans. In: *The cutting edge: New approaches to the archaeology of human origins*, ed. K. Schick & N. Toth, pp. 207–65. Stone Age Institute Press. [RLH]
Stout, D., Toth, N., Schick, K. & Chaminade, T. (2008) Neural correlates of early Stone Age toolmaking: Technology, language and cognition in human evolution. *Philosophical Transactions of the Royal Society B* 363(1499):1939–49. [aKV, GV]
Stout, D., Toth, N., Schick, K. & Chaminade, T. (2009) Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. In: *The sapient mind: Archaeology meets neuroscience*, ed. C. Renfrew, C. Frith & L. Malafouris, pp. 1–19. Cambridge University Press. [RLH]
Suddendorf, T. (2008) Explaining human cognitive autapomorphies. *Behavioral and Brain Sciences* 31(2):147–48. [LM]
Suddendorf, T. & Corballis, M. (1997) Mental time travel and the evolution of the human mind. *Genetic, Social and General Psychology* 123:133–67. [aKV]
Suddendorf, T. & Corballis, M. (2007) The evolution of foresight: What is mental time travel and is it unique to humans? *Behavioral and Brain Sciences* 30:299–351. [aKV]
Suddendorf, T. & Corballis, M. (2009) How great is ape foresight? *Animal Cognition* 12:751–54. [MO, aKV]
Suddendorf, T., Nielsen, M. & von Gehlen, R. (2011) Children's capacity to remember a novel problem and to secure its future solution. *Developmental Science* 14:26–33. [MN]
Szolonsky, A. (2006) Object use in pretend play: Symbolic or functional? In: *Doing things with things*, ed. A. Costall & O. Dreier, pp. 67–85. Ashgate Publishing. [AR]
Taylor, A., Elliffe, D., Hunt, G. & Gray, R. (2010) Complex cognition and behavioural innovation in New Caledonian crows. *Proceedings of the Royal Society B: Biological Sciences* 277(1694):2637–43. [EMP, AHT]
Taylor, A. H., Hunt, G. R., Medina, F. S., Gray, R. D. (2009a) Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society B: Biological Sciences* 276:247–54. [EMP, AHT]
Taylor, A. H., Hunt, G. R., Roberts, R., Gray, R. D. (2009b) Causal reasoning in New Caledonian crows: Ruling out spatial analogies and sampling error. *Communicative & Integrative Biology* 2:311–12. [AHT]
Tebbich, S. & Bshary, R. (2004) Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Animal Behaviour* 67:689–97. [AHT]
Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D. (2001) Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society B: Biological Sciences* 268(1482):2189–96. [EMP, SMR]
Tebbich, S., Taborsky, M., Fessl, B. & Dvorak, M. (2002) The ecology of tool-use in the woodpecker finch *Cactospiza pallida*. *Ecology Letters* 5:656–64. [SMR]
Tenenbaum, J. B., Griffiths, T. L. & Kemp, C. (2006) Theory-based Bayesian models of inductive learning and reasoning. *Trends in Cognitive Sciences* 10(7):309–18. [DCP]
Tennie, C., Call, J. & Tomasello, M. (2009) Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364(1528):2405–15. [CT, aKV]
Tennie, C., Call, J. & Tomasello, M. (2010) Evidence for emulation in chimpanzees in social settings using the floating peanut task. *PLoS ONE* 5(5):e10544. [AR]
Tennie, C., Hedwig, D., Call, J. & Tomasello, M. (2008) An experimental study of nettle feeding in captive gorillas. *American Journal of Primatology* 70(6):584–93. [POJ]
Tetzlaff, M. & Carruthers, P. (2008) Languages of thought need to be distinguished from learning mechanisms, and nothing yet rules out multiple distinctively human learning systems. *Behavioral and Brain Sciences* 31:148–49. [DCP]
Thornton, A. & McAuliffe, K. (2006) Teaching in wild meerkats. *Science* 313(5784):227–29. [EMP]
Thornton, A. & Raihani, N. J. (2011) Identifying teaching in wild animals. *Learning & Behavior* 38:297–309. [SMR]
Tobach, E., Falmagne, R. J., Parlee, M. B., Martin, L. M. W. & Scribner Kapelman, A. (1997) *Mind and social practice: Selected writings of Sylvia Scribner.* Cambridge University Press. [SR]
Toelch, U., Bruce, M. J., Meeus, M. T. H. & Reader, S. M. (2011) Social performance cues induce behavioral flexibility in humans. *Frontiers in Psychology* 2:160. [SMR]
Tomasello, M. (1990) Cultural transmission in the tool use and communicatory signaling of chimpanzees. In: *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives*, ed. S. Parker & K. Gibson, pp. 274–311. Cambridge University Press. [aKV]
Tomasello, M. (1994) The question of chimpanzee culture. In: *Chimpanzee cultures*, ed. W. Wrangham, W. McGrew & F. de Waal, pp. 301–17. Harvard University Press. [aKV]
Tomasello, M. (1999) *The cultural origins of human cognition*. Harvard University Press. [AR, CT]
Tomasello, M. (2000) Two hypotheses about primate cognition. In: *The evolution of cognition*, ed. C. Heyes & L. Huber, pp. 165–83. MIT Press. [aKV]
Tomasello, M. (2009) Postscript: Chimpanzee culture. In: *The question of animal culture*, ed. K. N. Laland & B. G. Galef, pp. 213–21. Harvard University Press. [aKV]
Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. (2005) Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences* 28(5):675–735. [LM, MO, aKV]
Tomasello, M., Davis-Dasilva, M. & Camak, L. (1987) Observational learning of tool-use by young chimpanzees. *Human Evolution* 2:175–83. [aKV]
Tomasello, M. & Herrmann, E. (2010) Ape and human cognition: What's the difference? *Current Directions in Psychological Science* 19:3–8. [LM, aKV]
Tomasello, M., Kruger, A. C. & Ratner, H. H. (1993) Cultural learning. *Behavioral and Brain Sciences* 16:495–511. [aKV]
Tomonaga, M. (2008) Relative numerosity discrimination by chimpanzees (Pan troglodytes): Evidence for approximate numerical representations. *Animal Cognition* 11:43–57. [aKV]
Toth, N. & Schick, K. (1993) Early stone industries and inferences regarding language and cognition. In: *Tools, language, and cognition in human evolution*, ed. K. Gibson & T. Ingold, pp. 346–62. Cambridge University Press. [aKV]
Toth, N. & Schick, K. (2009) The Oldowan: The tool making of early hominins and chimpanzees compared. *Annual Review of Anthropology* 38(1):289–305. [aKV]
Toth, N. & Schick, K. (2010) Hominin brain reorganization, technological change, and cognitive complexity. In: *The human brain evolving: Paleoneurological studies in honor of Ralph L. Holloway*, ed. D. C. Broadfield, M. Yuan, K. Schick & N. Toth, pp. 293–312. (chap. 19). Stone Age Institute Press. [RLH]
Trivers, R. (1971) The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57. [aKV]
Umiltà, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F. & Rizzolatti, G. (2008) When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences* 105(6):2209–13. [MAA]
Uomini, N. (2009) The prehistory of handedness: Archaeological data and comparative ethology. *Journal of Human Evolution* 57:411–19. [aKV]
Vaesen, K. (2011) The functional bias in the dual nature of technical artefacts program. *Studies in History and Philosophy of Science* 42:190–97. [AR]
Vaesen, K. (2012) The cognitive bases of human tool use. Behavioral and Brain Science 35(4). [HIJ]

van de Waal, E., Renevey, N., Favre, C. M. & Bshary, R. (2010) Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences* 277:2105–11. [SMR]

van Schaik, C. P., Deaner, R. O. & Merrill, M. Y. (1999) The conditions for tool use in primates: Implications for the evolution of material culture. *Journal of Human Evolution* 36:719–41. [SMR]

van Schaik, C. P. & Pradhan, G. R. (2003) A model for tool-use traditions in primates: Implications for the coevolution of culture and cognition. *Journal of Human Evolution* 44(6):645–64. [CT]

Vander Wall, S. B., Enders, M. S. & Waitman, B. A. (2009) Asymmetrical cache pilfering between yellow pine chipmunks and golden-mantled ground squirrels. *Animal Behaviour* 78(2):555–61. [EMP]

Vanduffel, W., Fize, D., Peuskens, H., Denys, K., Sunaert, S., Todd, J. T. & Orban, G. A. (2002) Extracting 3D from motion: differences in human and monkey intraparietal cortex. *Science* 298:413–15. [GAO]

Verhagen, A. (2005) *Constructions of intersubjectivity: Discourse, syntax, and cognition*. Oxford University Press. [MAA]

Vingerhoets, G., Alderweireldt, A.-S., Vandemaele, P., Cai, Q., Van der Haegen, L., Brysbaert, M. & Achten, E. (in press) Praxis and language are linked: Evidence from co-lateralization in individuals with atypical language dominance. *Cortex* [GV]

Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M. G. & Andrade, F. R. D. (2007) Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology* 132:426–44. [TN]

Visalberghi, E. & Limongelli, L. (1994) Lack of comprehension of cause–effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 108(1):15–22. [AHT, aKV]

Visalberghi, E. & Tomasello, M. (1998) Primate causal understanding in the physical and psychological domains. *Behavioral Processes* 42:189–203. [aKV]

Vonk, J. & Povinelli, D. J. (2006) Similarity and difference in the conceptual systems of primates: The unobservability hypothesis. In: *Comparative cognition: Experimental explorations of animal intelligence*, ed. E. M. Wassermann & T. R. Zentall, pp. 363–87. Oxford University Press. [AHT]

Vygotsky, L. S. (1933/1967) Play and its role in the mental development of the child. *Soviet Psychology* 5:6–18. [AR]

Wadley, L. (2005) Putting ochre to the test: Replication studies of adhesives that may have been used for hafting tools in the Middle Stone Age. *Journal of Human Evolution* 49:587–601. [LB-C]

Waldmann, M. & Holyoak, K. (1992) Predictive and diagnostic learning within causal models: Asymmetries in cue competition. *Journal of Experimental Psychology* 121:222–36. [rKV]

Waldmann, M., Holyoak, K. & Fratianne, A. (1995) Causal models and the acquisition of category structure. *Journal of Experimental Psychology* 124:181–206. [rKV]

Walker, A. (2009) The strength of great apes and the speed of humans. *Current Anthropology* 50:229–35. [arKV]

Walsh, V. (2003) A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences* 7(11):483–88. [GV]

Want, S. & Harris, P. (2001) Learning from other people's mistakes: Causal understanding in learning to use a tool. *Child Development* 72:431–43. [aKV]

Warneken, F. & Tomasello, M. (2006) Altruistic helping in human infants and young chimpanzees. *Science* 311:1301–303. [aKV]

Washburn, S. L. (1959) Speculations on the interrelations of the history of tools and biological evolution. *Human Biology* 31:21–31. [PBC]

Weir, A. A. S., Chappell, J. & Kacelnik, A. (2002) Shaping of hooks in New Caledonian crows. *Science* 297(5583):981. doi: 10.1126/science.1073433 [MAA, SRB, rKV]

Weiss, D. J. & Wark, J. (2009) Hysteresis effects in a motor task in cotton-top tamarins (*Saguinus oedipus*). *Journal of Experimental Psychology: Animal Behavior Processes* 35:427–33. [DJW]

Weiss, D. J., Wark, J. D. & Rosenbaum, D. A. (2007) Monkey see, monkey plan, monkey do: The end-state comfort effect in cotton-top tamarins (*Saguinus oedipus*). *Psychological Science* 18(12):1063–68. [POJ, DJW]

Wellman, H. M., Cross, D. & Watson, J. (2001) Meta-analysis of theory-of-mind development: The truth about false belief. *Child Development* 72:655–84. [MN]

Wheeler, M. & Clark, A. (2008) Culture, embodiment and genes: Unravelling the triple helix. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:3563–75. [LM]

Whiten, A., Custance, D., Gomez, J., Teixidor, P. & Bard, K. (1996) Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology* 110:3–14. [aKV]

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. (1999) Cultures in chimpanzees. *Nature* 399:682–85. [AB, CT]

Whiten, A., Horner, V. & de Waal, F. (2005) Conformity to cultural norms of tool use in chimpanzees. *Nature* 437:738–40. [EMP, arKV]

Whiten, A., Horner, V. & Marshall-Pescini, S. (2003) Cultural panthropology. *Evolutionary Anthropology* 12:92–105. [aKV]

Whiten, A., McGuigan, N., Marshall-Pescini, S. & Hopper, L. (2009) Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B* 364:2417–28. [CT, aKV]

Whiten, A., Spiteri, A., Horner, V., Bonnie, K., Lambeth, S., Schapiro, S. & de Waal, F. (2007) Transmission of multiple traditions within and between chimpanzee groups. *Current Biology* 17:1–6. [aKV]

Willems, R. M., Toni, I., Hagoort, P. & Casasanto, D. (2010) Neural dissociations between action verb understanding and motor imagery. *Journal of Cognitive Neuroscience* 22:387–400. [GG]

Wolpert, L. (2003) Causal belief and the origins of technology. *Philosophical Transactions: Mathematical, Physical and Engineering Sciences* 361(1809):1709–19. [aKV]

Wynn, T. (1981) The intelligence of Oldowan hominids. *Journal of Human Evolution* 10:529–41. [aKV]

Wynn, T. (2002) Archaeology and cognitive evolution. *Behavioral and Brain Sciences* 25:389–438. [aKV]

Wynn, T. & Coolidge, F. (2007) Did a small but significant enhancement in working memory capacity power the evolution of modern thinking? In: *Rethinking the human revolution*, ed. P. Mellars, K. Boyle, O. Bar-Yosef & C. Stringer, pp. 79–90. McDonald Institute Monographs. [aKV]

Xitco, M. J., Gory, J. D. & Kuczaj, S. A. (2004) Dolphin pointing is linked to the attentional behavior of a receiver. *Animal Cognition* 7(4):231–38. [EMP]

Zelazo, P. D., Jacques, S., Burack, J. A. & Frye, D. (2002) The relation between theory of mind and rule use: Evidence from persons with autism-spectrum disorders. *Infant and Child Development* 11:171–95. [DCP]

Zwaan, R. & Taylor, L. J. (2006) Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology: General* 135:1–11. [HIJ]